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CONTENTS

A LIMNOLOGICAL STUDY OF ERH HAI, YUNNAN, CHINA:

PHYSICO-CHEMICAL CHARACTERISTICS

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(With 4 Figures in the Text)

1. INTRODUCTION

Of the numerous lakes in China not a single one, as far as can be ascertained, has been studied limnologically. By virtue of its nearness to Erh Hai this laboratory found an excellent chance to make a study of this lake while we sought refuge in this backward region in the south-west of Yunnan. Limitations of research facilities and lack of co-operation made the progress of this study distressingly slow. It is the purpose of this first paper to report on the data so far obtained, under these conditions, on the physico-chemical characteristics of this lake. Other aspects of this limnological study are still under investigation (which we hope will be permitted to continue) and will be reported later.

2. MORPHOMETRY OF ERH HAI

Erh Hai is a large, fresh-water lake in the Tali Valley. This valley is about 26 miles long, situated at about 100° E. long. and 25° 35′ to 58′ N. lat. It is bounded on the west by the Tien Chang Mountain range which rises about 14,000 ft. above sea-level and on the east by a much lower range of mountains, the Tung San, about 9000–10,000 ft. above sea-level. At the northern end of the valley these two mountain ranges approach each other, leaving a narrow gap for the inlet of lake Erh Hai. The southern end of the valley is slightly wider than the northern and is also bordered by a comparatively low range of mountains. The valley itself is 6675 ft. above sea-level (U.S. Army data). The western portion of this valley consists of an alluvial plain and terraced hillsides which give place to boulder cones and fans leading to the foothills of the Tien Chang Mountain. Ehr Hai occupies the eastern half of the valley. Like the valley, the lake itself is elongated, with its long axis running in a north-north-west direction. By applying Simpson's rule for finding the area of an irregular surface to the map of Erh Hai,* shown in

* We are much obliged to the Yunnan Bureau of Construction for the use of the map of Erh Hai, which was surveyed in 1943. Fig. 1 is directly reduced from the Bureau's blue prints. The Simpson's formula used is:

$$A = \tfrac{1}{3}h\,[(y_0 + y_n) + 4\,(y_1 + y_3 + \ldots) + 2\,(y_2 + y_4 + \ldots)],$$

where $y_0, y_1, y_2, \ldots, y_n$ are the 1st, 2nd, 3rd, ..., $(n+1)$th parallels drawn at equal distance apart across the map, and h is the distance between any two of these $n+1$ parallels.

Fig. 1, the total area of this lake is found to be about 259 sq. km. or about 100 sq. miles. The lake is about 26 statute miles, or 42 km., in length. The maximum width of the lake is about 9·12 km., and it is slightly more than 3 km. across its narrowest part, its mean width being 5·96 km. (or 3·7 miles).

This lake is supplied from the north by the Erh River. The extensive delta formed by this river at the entrance to the lake has been turned into meadow and farm land. Upon this alluvial flat, which represents what used to be the northern portion of the lake, a viaduct has been constructed by the inhabitants. The *Tali Gazetteer* (1915) gives the names of eighteen streams conducting water from Tien Chang Mountain on the west into the lake, of one stream, Lao Tai Ching, from the east, and of another, Po Lo River, from Chao Haien on the south-eastern corner of Erh Hai. During the rainy season many temporary streams empty into the lake from all sides. Water of Erh Hai leaves the basin on its south-western corner at Sia Kuan, and, after merging with the Yangpi River, flows into the Mekong which runs into the China Sea. FitzGerald (1942) has given a number of fine photographs to show the outlet of this lake. There were three islands on the eastern side of the lake. But at the present only two of these three islands can be identified. The *Tali Gazetteer* recognizes four sand bars and nine bays in the lake.

For bathymetric data lead soundings were used in this investigation. In Fig. 1 the numbers on the map of Erh Hai indicate depth in metres along several sections across the lake and at a few interesting points. In vertical sections Erh Hai appears skewed, with its greatest depth on the eastern side of the basin (see Fig. 2). In these vertical sections the depth has been exaggerated 135 times in comparison with the east–west distance. On the whole, deeper water occurs in the eastern half of the lake, and, as far as this survey shows, the northern quarter is shallower than the rest of the lake. The maximum depth of the lake found by lead sounding is 20·75 m. at the eastern end of section FE (see Fig. 1). According to local fishermen who have extensive fishing experience in Erh Hai, the place where we found the maximum depth is also the deepest part of the lake in their opinion, while all the other regions are shallower.

FIG. I — ERH HAI (map)

1·7 1·4
1·5 2·1
5·7
6·0 7·
8·0

5·35 12·3 B
·4·9 8·3
A 8 3
1·9· 1 2
1·7· 5 7
D 9·8 C
2
1 3 12 13·3
15 17·75 18·3
2·25 11·5 17 20·75 E
1·5 2 4·25
F1

0·9
1·97 0·9
2 9·5 8·5 7·75
G 2 4 8 H

15
10·3

ERH HAI

5·2
10·3

Metres
0   2000

11·16
2·3 6·7

Table 1. *Vertical distribution of temperature in Erh Hai at different times of the year* (1942–3)

Date	Hour	Section and station	Depth (m.)	Temp. °C.
18 July	10.00–10.11	Sect. FE: St. 1	0	23·7
			3	23·1
			7	23·4
			10	22·8
	12.17–12.22	St. 2	0	24·7
			3·25	24·05
			5	22·10
10 Aug.	11.05–11.15	St. 3	0	24·8
			9·5	23·1
			11·25	23·1
			13·25	24·2
	11.45–12.24	St. 4	0	26·0
			4·25	24·8
			6·25	23·3
			8·75	25·3
	12.49		0	25·7
	13.05–13.27	St. 5	0	26·0
			3	23·8
			1·5	24·5
			5·5	23·5
	16.09–16.19	St. 6	0	26·55
			9·5	23·2
			12·5	23·02
			17	25·8
	16.41–16.49	St. 7	0	26·25
			4·5	23·3
			8·5	23·2
			18·5	26·0
31 Aug.	13.20–13.45	St. 8	0	23·5
			3·75	23·0
			16·75	22·8
			19·75	22·9
	14.08–14.18	St. 9	0	24·2
			5	22·9
			7·5	22·8
			10·5	22·8
	18.30	St. 10	0	23·6
10 Oct.	15.40–16.15	Sect. GH: St. 1	0	21·8
			1·75	21·7
			4	20·75
			6·75	21·7
11 Oct.	7.40– 8.23	St. 2	0	20·9
			1·5	19·98
			2·5	20·75
			3·5	20·85
			4·5	20·7
	9.10– 9.23	St. 3	0	21·5
			2	20·85
			4	20·75
			7	20·65
	11.03–11.13	St. 4	0	23·55
			3	20·8
			5	20·78
			7·5	20·62
	12.03–12.13	St. 5	0	23·2
			3	21·1
			6	20·69
			9	20·65
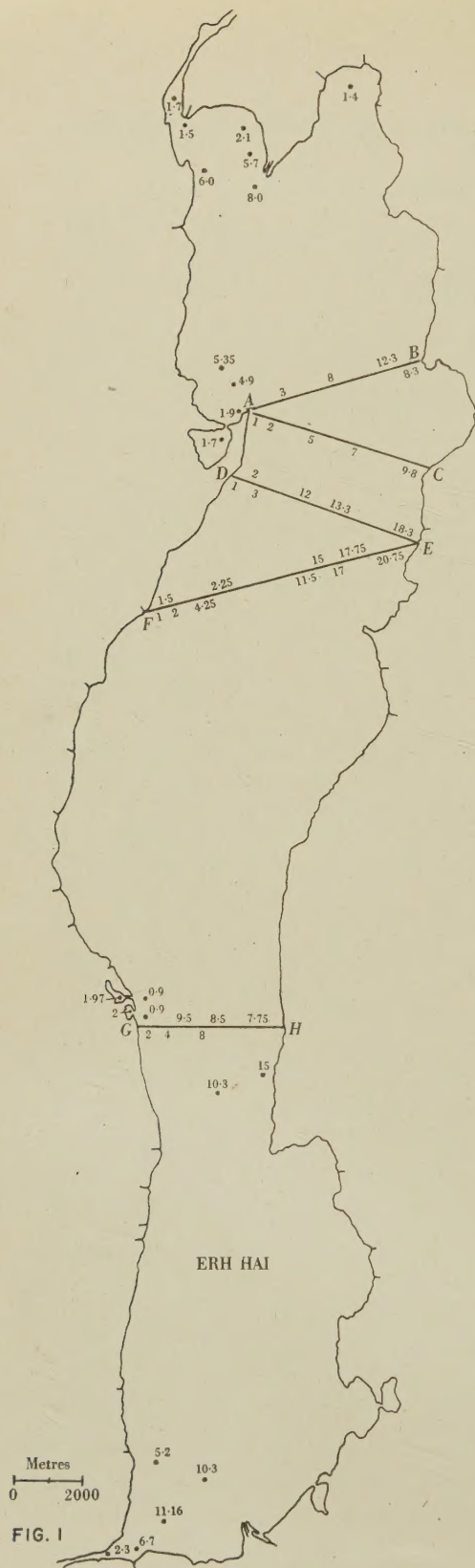
Table 1 (continued)

Date	Hour	Section and station	Depth (m.)	Temp. ° C.
29 Nov.	11.15–11.55	Sect. DE: St. 1	0	16·65
			2	16·4
			3·75	16·1
			4·5	16·1
			5	16·1
			6·75	16·0
			7	16·1
			7·5	16·1
			10	16·1
	14.00–14.10	St. 2	0	16·5
			5·5	16·0
			9·75	16·0
			14	16·0
30 Mar.	8.10	Sect. FE: St. 1	0	12·05
	8.50– 9.50	St. 2	0	13·9
			1	13·4
			2	13·25
			3	13·25
			4	12·8
			5	12·7
			6	12·65
			7	12·65
			8	12·55
			9	12·55
	11.35	St. 1	0	14·7
	13.20–14.00	St. 2	0	18·2
			1	14·2
			2	13·4
			3	13·2
			4	13·1
			5	12·9
			6	12·8
			7	12·8
			10	12·7
	14.50	St. 3	0	16·2
	14.55–15.10	St. 4	0	17·6
			1	14·4
			2	13·7
			3	13·5
			4	13·3
			5	13·2
			6	13·1
			8	12·8
			10	12·7
			12	12·7
	15.20		0	17·4
28 Apr.	11.50–12.38	Sect. DE: St. 1	0	17·80
			8	16·50
			8·2	16·90
			9·13	16·90
10 May	11.50	St. 2	0	19·4
			1·25	18·6
	18.37		0	20·6
			1·25	19·0

Strong littoral development with abundant vegetation is seen along the entire western side of the lake, while on the east such development is very limited. There is a rocky shoal 1–2 m. below the surface a short distance to the south-east of Tali. The shore-line is slightly better developed on the east than on the west side—its development (ratio between north-south shore-line length and a straight line starting and ending at the same points as the shore-line) amounts to 1·58 on the east and 1·43 on the west side. The total length of the shore-line of Erh Hai is 137·35 km. (about 85 miles). The development of the total shore-line, i.e. the ratio of the shore-line to the circumference of a circle whose area is equal to that of the lake, is 2·435.

On the north and west side the shallow basin of Erh Hai merges gradually—the slope of shoal bottom is very slight—into alluvial plains on which wave action has created many beaches. The small marginal slope on the west side makes its margin much less definite than on the east. Interspersed among the sandy beaches on the west there are many low-lying swamp, bog, or marsh areas.

3. THERMAL CONDITIONS

In studying the distribution of temperature in this lake reversing thermometers were used. Each thermometer was mounted on a frame which reversed itself as soon as a messenger, sent from on board the ship, struck the releasing mechanism on top of the frame. Thermal data obtained from different stations at different depths and at different times of the year are summarized in Table 1. It will be seen from this table, as well as from Figs. 3 and 4, that there is no clear-cut thermal stratification with an epilimnion and hypolimnion separated by a thermocline at any time of the year. With the exception of the very top 1–2 m. layer, the temperature throughout each water column is, on the whole, very uniform. Subsurface temperature, from 3 m. down to the bottom, shows an annual variation, being highest in August and lowest in March. Thus, the mean subsurface temperatures for July, August, September, October, November, March and April are 23·09, 24·04, 22·87, 20·78, 16·05, 12·82 and 16·63° C. The surface temperature is also highest in August and lowest in March. The average value of surface temperature for August is 25·66° C. and that for March is 15·72° C. Figs. 3 and 4 show some temperature-depth curves for these two months. In neither month is there a stable stratification built up by insolation.

Diurnal change of water temperature takes place most noticeably in the first metre layer. Insolation can produce an increase in the temperature of this layer amounting to 3–4° C. Generally, temperature of surface water is lowest in the morning—between 6 and 8 a.m.—and increases gradually in the forenoon and more rapidly in the afternoon until the

maximum is reached between 3 and 4 p.m. It then drops gradually, and heat is partly conducted downward by vertical mixing and partly by removal from the surface by air. In March, the coldest time, the difference between the water temperature of the first and second metre is less than 0·5° C. in the morning (see curve 4 in Fig. 4), at noon, curve 5, the surface water is 1° warmer than that at the second metre, while by 3 p.m., curve 6, this difference has become as great as 4°. In the warmest time of the year, in August, this warming up of the surface layer is also obvious when curve 1 in Fig. 3 based on observations made in the morning is compared with curve 2 made from afternoon data of the same day.

4. CHEMISTRY OF THE WATER

In this report the chlorinity, oxygen content and H-ion concentration only are included. The usual oceanographic method was used to determine the chlorinity of water from different parts of this lake. In this method the total halides were titrated against standard silver nitrate solution, using potassium chromate as indicator, and the result expressed as chloride ions in parts per million (p.p.m.). There is no significant variation in the chlorinity of water of this lake from different parts of the basin and at different times of the year. The mean value of chlorinity was 46·13 p.p.m.

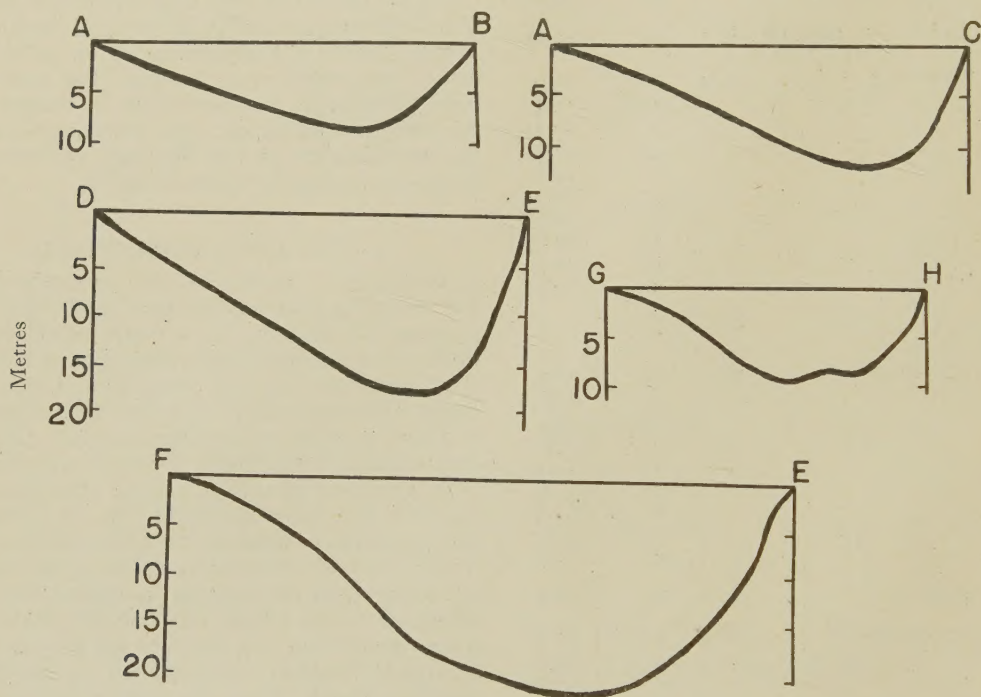By using specially constructed water bottles,

Fig. 2. Vertical sections of Erh Hai.

Change in the temperature of the surface water of the lake follows that of the air temperature and depends upon the effect of insolation. This is shown in Fig. 3. On 31 August, curve 3 in Fig. 3, the weather was cloudy and windy, with an air temperature of 24° C. at 2–3 p.m. and there was very little difference between the temperature of the first metre layer and the rest of the water column, in contrast to the condition seen on 10 August, curve 2, when the air temperature was 26° C. and the sky clear. The uniformity of the temperature of the entire water column shows how effective vertical mixing is in this lake during a windy day.

samples of water from different depths in Erh Hai at different stations were secured. To examine the dissolved oxygen content each sample was subjected to the standard method (Anon., 1936) for oxygen determination. The results were expressed both as c.c. of dissolved O_2 per litre of water at N.T.P. and as parts per million under the same conditions. The solubility values of oxygen in fresh water at various temperatures and exposed to an atmosphere containing 20·9 % oxygen under 760 mm. pressure, calculated by Whipple & Whipple (1911) from the measurements of Fox (1909), were again corrected so as to apply to our local condition where the

barometric pressure at o° C. is only 590 mm. By comparison with these latter corrected values the percentage of oxygen saturation was calculated for each water sample. The data on oxygen contents of water samples examined are shown in Table 2. Generally speaking, the content of dissolved oxygen in the surface layer of Erh Hai water varies from of the year. Regionally, water of the littoral region has higher oxygen content than offshore water. This is apparently due to the presence of large quantities of attached plants in the shallower water, besides phytoplankton common to both littoral and limnetic regions. When the oxygen contents of different strata of water are compared it is seen that for each
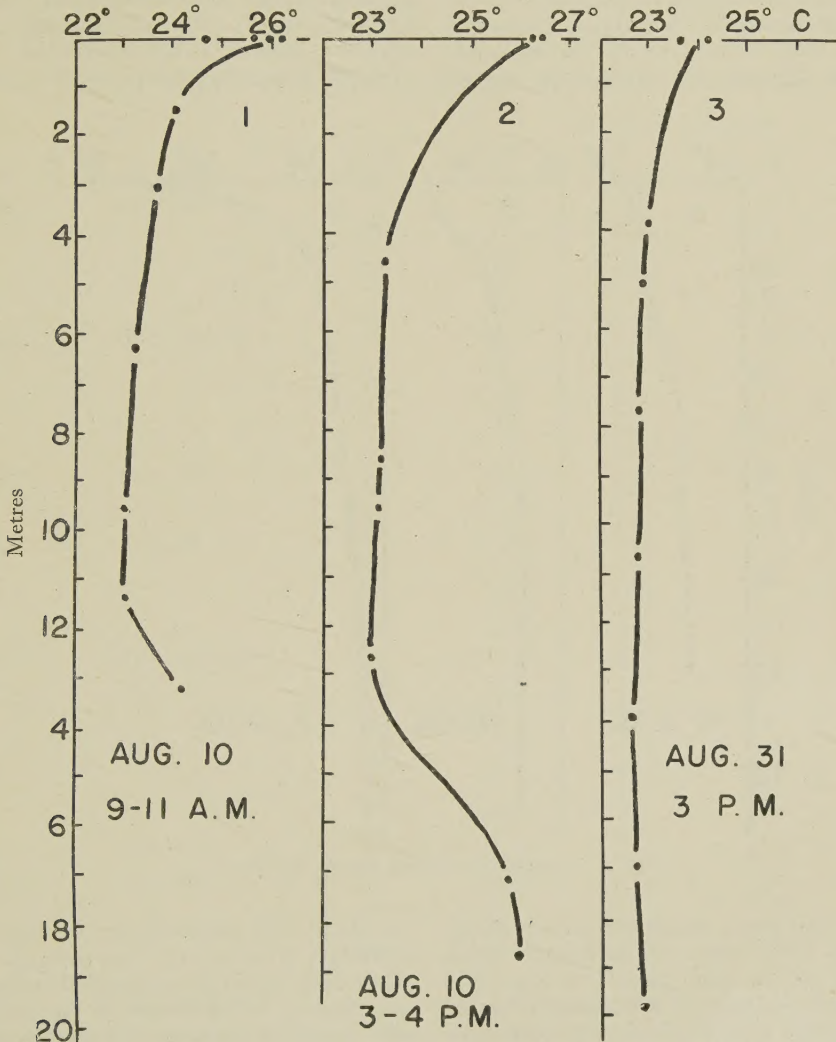
Fig. 3. Temperature-depth curves.

5·43 to 4·42 c.c./l. (i.e. 7·78–6·29 p.p.m.). The oxygen content of the surface layer as well as that of the deeper stratum is very high. The lowest value observed is 71·5 % saturation. With the exception of October data, it will be seen from Table 2 that the surface water is always supersaturated. Relatively speaking, October is the month when the oxygen content of the water is lower than in the other parts water column there is very little difference from one layer to another. There is no oxygen deficiency in any of the layers at the stations examined. The vertical distribution of oxygen agrees well with that of temperature. They both show little variation from top to bottom. This is a consequence of the thorough mixing of water of this shallow and open lake. No stratification to any considerable extent is seen.

The H-ion concentration of Erh Hai water was determined in the field colorimetrically by means of Hellige colour disks and indicators. These colour disk readings were checked, before using, with buffered solutions titrated with quinhydrone electrodes in the laboratory. The pH values of limnetic and littoral waters of this lake were found to be fairly similar, ranging from pH 8·0 to 8·4. But on the west side of the lake in the shallow, partially enclosed bay, popularly known as the Lung Hu, and separated from the main body of water by the peninsula AD (see Fig. 1), the pH value was found to be between

delta at the inlet, the deposition of foreset and topset beds and the decrease of the lake's depth by the accumulation of bottom sets all indicate that Erh Hai has grown much smaller and shallower and is probably on the decline in its life history. However, it would be of great interest to secure cores of the bottom deposits of the lake. We are trying to look for ways and means of getting a core sampler.

According to Thienemann (1926, 1931), as quoted by Welch (1935), most eutrophic lakes have a mean depth less than 18 m. Erh Hai is a shallow open body of water whose average depth is much less than 18 m.
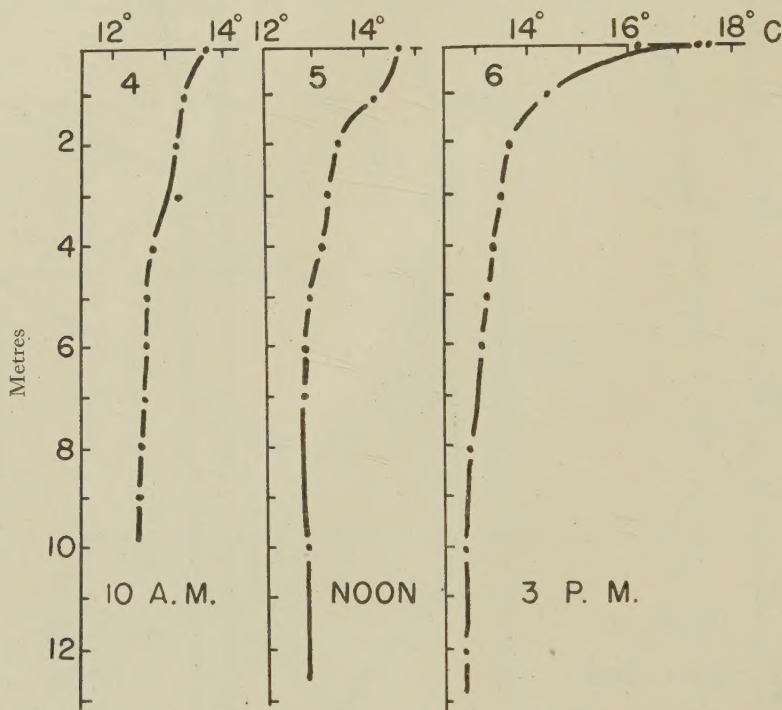
Fig. 4. Temperature-depth curves, 30 March.

9·05 and 9·10. This bay is always very rich in plankton as well as in littoral forms of rooted plants which grow profusely all the year round over the whole bottom of the bay, and most of them are as tall as the depth of the water. Here the oxygen content of the water is also very high. The dissolved oxygen amounts to 6·8–7·8 c.c./l., that is, 9·7–11 p.p.m., corresponding to 144–162 % saturation.

5. DISCUSSION

Visiting geologists tell us that Erh Hai was formed by folding probably during the mid-Tertiary at the time of Himalayan uplifting. In addition to occasional remnants of abandoned shore-lines during the dwindling of the lake, the formation of an extensive

On the physico-chemical side, the high productivity of the lake is indicated by the thorough mixing of the water, high oxygen content and pH value. Of course, quantitative determination of the nutrients and of zoo- and phytoplankton will give better support to this point.

The morphometric features, the distribution of temperature and oxygen all agree in showing that Erh Hai belongs to the class of temperate lakes of the third order, according to the classification of Forel as modified by Whipple (1927).

From November until the rainy season, which generally begins between May and June, there is constant wind in this valley, and very often it reaches gale strength. During other times of the year the

wind is not so constant. This long windy period is most likely responsible for the thorough mixing of Erh Hai water in all directions.

The annual heat budget calculated according to the method of Birge amounts to 12,000–18,000 g.cal./sq.cm. This is much lower than the value for American and European lakes (Welch, 1935; Birge, 1915) and even lower than the 22,000–26,000 range of western Tibetan lakes twice as high as this lake (Hutchinson, 1937).

March. The annual range of mean subsurface temperature is 24·04–12·82° C. The annual heat budget is estimated at 12,000–18,000 g.cal./sq.cm. Diurnal change in temperature is most noticeable in the surface layer, but vigorous vertical mixing conveys the heat from the surface to the bottom very effectively. There is no stratification, the subsurface temperature being fairly uniform.

3. Erh Hai water has a chlorinity of 46·13 p.p.m. Its oxygen content varies between 3·5 and 5·4 c.c./l.

Table 2. *Measurement of dissolved oxygen in water samples from Erh Hai*

Date	Place	Depth (m.)	Temp. ° C.	Dissolved oxygen c.c./l.	Dissolved oxygen P.p.m.	% saturation
28 Apr.	Sect. AB: St. 1	0	17·8	5·28	7·58	102
		8	16·5	5·01	7·17	93·5
	St. 2	0	18·0	5·35	7·67	103·2
		8·3	16·9	4·93	7·08	93·4
	St. 3	0	18·0	5·26	7·55	103·5
		9·8	16·8	5·42	7·76	102·1
10 May	Sect. DE: St. 1	0	18·2	5·28	7·58	102·2
		1	18·2	5·24	7·5	101·2
	St. 2	0	19·4	5·01	7·17	100
		1	18·6	4·60	6·59	89·7
	St. 3	0	20·6	5·08	7·28	103·3
		1	19·0	5·15	7·37	101·3
2 July	Sect. FE	0	24·5	5·43	7·78	118·5 (?)
		10	22·8	4·64	6·65	92·5
		12	24·4	4·7	6·73	96·4
10 Aug.	Sect. FE	0	24·8	4·58	6·57	101·1
		3	23·8	4·73	6·78	102
		5·5	23·5	4·59	6·58	98·7
		9	25·3	4·52	6·47	99·6
		13	24·2	4·65	6·66	98·8
10 Oct.	Sect. GH: St. 1	0	21·8	4·88	6·96	100·8
		1·8	21·7	4·96	7·07	102·3
		6·8	21·7	5·04	7·19	104
	St. 2	0	20·9	4·42	6·29	90
		2·5	20·7	4·52	6·45	92·2
		4·5	20·7	4·23	6·06	86·5
	St. 3	0	21·5	4·52	6·47	93·6
		2	20·85	3·50	5·00	71·5
		4	20·75	4·49	6·43	91·9
		7	20·65	4·70	6·73	95·8
11 Oct.	Sect. GH	0	23·35	4·53	6·49	98·2
		3	20·8	4·59	6·59	95·5
		5	20·78	3·63	5·24	75·9
		7·5	20·62	4·64	6·65	95

6. SUMMARY

1. Erh Hai is an elongated fresh-water lake, 2034 m. (6675 ft.) above sea-level. It is situated at 25° 35'–58' N. and 100° 6'–19' E., and has an area of about 259 sq.km. (100 sq. miles). Its basin is shallower on the west and deeper on the east side, where the maximum depth reaches 20·75 m. Its mean depth is 10–15 m. There is strong littoral development on the western side, while the eastern shore is much steeper and consists mainly of wave-cut cliffs.

2. The water is warmest in August and coolest in

(5–7·8 p.p.m.). There is no oxygen deficiency, but supersaturation is the rule in the surface layer. In the subsurface layers the variations in dissolved oxygen are very small.

4. In the lemnetic water H-ion concentration also shows little variation. The pH value is 8·0–8·4. But in enclosed bays with abundant growth of plants, both benthic and planktonic, the pH value is higher— 9·05–9·10.

5. Reasons are given for considering Erh Hai an eutrophic lake of the temperate class of the third order.

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AN EXAMINATION OF THE POLLEN LOADS OF *ANDRENA*: THE SPECIES THAT VISIT FRUIT TREES

By V. H. CHAMBERS

(With 1 Figure in the Text)

1. INTRODUCTION

Few ecological studies of the solitary bees of the genus *Andrena* Fabricius have been made in Britain, which is rather surprising as most of the sixty or more species are comparatively large insects, many are abundant on flowers, and the individual species are not difficult to separate. On the other hand, our general knowledge of the genus and distribution of the species is quite substantial, as, in addition to the outstanding paper by Perkins (1919), there are a large number of records in the county lists and in notes scattered throughout the literature. From these sources it is known that some species are found only in certain types of localities and ecological formations, others have a limited geographical distribution, and that a considerable number are rare or erratic in appearance. In addition, observations have been made upon the flowers visited by the different species: here again, hymenopterists have emphasized the special peculiarities and limited choice of flowers visited even by some of the commoner species. The information available, although extensive, is limited in depth and mainly descriptive without a quantitative basis. With the object of attempting to gain more precise knowledge this work was begun during 1941, the present paper being of an introductory nature.

Many factors govern the distribution and abundance of *Andrena* species. These may include edaphic factors such as geological origin, texture and particle size of soil, its properties of water retention, all of which will have their influence in any particular soil mass upon its drainage, cohesion and physical stability, of importance to fossorial Hymenoptera in the selection of burrow sites. The sources of larval food—pollen and nectar—are the next concern of the bee after completion of its burrow, and it is with the first of these that I shall be concerned. Here again, to my knowledge, we do not know what are the relative proportions of these two constituents required in the larval diet, but this is a physiological rather than an ecological question, and no attempt will be made at present to supply an answer. Even if only these two categories of soil and larval food are considered, it is perhaps not too sweeping to state that human operations, e.g. drainage, deafforestation and the expansion of agriculture, have

had a greater effect upon the distribution and population of fossorial Hymenoptera than upon other orders of insects. The present *Andrena* fauna can therefore be considered to be in a sense 'artificial' and in a state of instability as regards the numerical representation of species and individuals in each species. A study of the plants foraged for may therefore give some guide as to the adaptability of a species and, by correlation with changes in the flora, may enable an interpretation of the present distribution of the species to be made.

Previous workers who have recorded the flowers visited by *Andrena* species have not always specified the sex of the individuals. It is highly probable that the males will visit any flower as long as it is a source of nectar, so that not much significance can be attached to observations made upon this sex, although in some species the males tend to frequent the same flowers as the females. Again, simple observations of flowers visited by the females are of less value than if the evident object of the visit, i.e. whether for pollen or nectar, had also been recorded. Furthermore, it is much more important to know not what flowers the females of a species will visit, however long the list, but what are their normal preferences at any one time or in any particular locality. Accurate counts of relative frequencies of visits made to different plant species furnish valuable results, but this method, which has been used by many early workers in classical studies upon the honey bee (see Clements & Long (1923) for a review of the early work), is laborious and difficult to apply to *Andrena*, as the females with their more rapid flight are difficult to follow, the species are much less numerous in individuals than the honey bee, and it would be wellnigh impossible to make counts on all the plants likely to be visited in a locality. Admittedly, as we have no method at present for the determination of the source of a sample of nectar, individual counts of visits are necessary to ascertain nectar preferences; and as I have already shown (1945) that visits may be made to flowers for pollen alone, it is quite probable that nectar may be taken from flowers either when the pollen is not available or it may be ignored.

On the other hand, the wide use of the technique of pollen analysis during the past few decades has

led to improvements in methods for the examination of pollen samples and increase in the knowledge of pollen morphology. Keys for the identification of pollen grains have been published in American and Continental literature but, with the exception of Allen (1937), little has been written upon the pollen of British plants. The determination of the species composition of pollen loads has been applied in the present work, to ascertain whether any selection of the available flora is made by the foraging *Andrena*.

A number of terms has been used, principally by American workers, to classify bees in general groups according to their foraging behaviour, these terms having been applied indifferently to describe visits to flowers or more specifically to the collection of pollen loads. Thus the term monotrophic (or -tropic) is applied to species of bees which restrict their visits to one species of plant, oligotrophic to those which only visit the flowers of a few closely related species (in the same genus or family), and polytrophic to those which visit a wide range of species. The modified terms mono-, oligo- and polylectic used by Robertson (1926) are etymologically more appropriate to describe pollen-collecting behaviour. These terms are suitable, if only as broad generalizations, to describe the behaviour of species of bees, and an examination of a large number of pollen loads from a species of *Andrena* will enable the appropriate descriptive term to be applied. As they stand, the terms polylectic, and to a lesser extent oligolectic, are not sufficiently precise in meaning, as they do not differentiate between the collection of pollen by separate individuals of a species at any one time or during the whole flight period from a variety of flowers and the collection of a variety of pollen species by a single individual on one foraging trip. In addition, the term constancy has been applied, usually in studies of the honey bee, to the behaviour of an individual female or worker in restricting successive visits to one species.

Clements & Long (1923) further subdivided the term: monodrome constancy to be applied to those cases where the bee visits the flowers of but one species during a single flight, and polydrome constancy to those where successive flights are always directed to the same species as long as this yields nectar or pollen. As distinct from the first three terms given above, these latter are descriptive of the behaviour of individuals and cannot be used as comparative indices of the behaviour of species, because the behaviour of an individual bee may be largely dependent upon its age and the foraging habits which it has acquired. The evidence in support of this last contention has been reviewed by Clements & Long. On the other hand, it is possible in some cases, by examination of a large number of pollen loads from separate individuals, to infer whether the individuals of a species exhibit either of these types of constancy.

It is admitted that these terms are only loosely descriptive, but they serve the purpose in the analysis of results—which inevitably must at first also be purely descriptive—of directing attention to varying degrees of deviation shown by different species from a hypothetical behaviour ideal. Later, upon the basis of sufficient data which I hope to present, it may be useful to employ fresh terms or to amend those already in use. I have not yet made any studies of the foraging behaviour of individuals of *Andrena* species, principally because of the great expenditure of time required by the work, as I have frequently recorded individual trips lasting $2\frac{1}{2}$ hr. or more even though the pollen was collected in good weather conditions and from flowers abundant in the immediate vicinity of the burrows. The emphasis of the work has been upon the behaviour of individuals in the aggregate of species in relationship to the flowers available rather than upon the response of individuals to individual flower species.

2. TECHNIQUE

To avoid imparting a bias to the results, the taking of individuals with pollen loads from flowers has, in general, been avoided, and unless otherwise stated, they were caught upon their return to their burrows. If taken from flowers, apart from the obvious selection, it is also likely that in many cases the insect would not have completed her load for the trip. This does not mean that a female will always return with a full load: frequently individuals have been observed to return with a miserable pinch of pollen even when the species is in full activity. On arrival at a colony all burrows are stopped with an inverted glass tube: this serves the purpose of preventing entry and of ascertaining whether the burrow is already occupied by the *Andrena*. This is hardly practicable or necessary in the case of species like *A. flavipes* Panz. which congregate in huge densely populated colonies. The returning bee, after capture, is enclosed in a cyanide tube for a few seconds until it has just lost the ability to stand, transferred immediately to a $2 \times \frac{1}{4}$ in. glass tube and kept in an upright position in the dark. Within 10 min. the bee will have recovered, and usually within about 30 min., presumably acting as if it were in its burrow, it will have removed its pollen load. In this way the pollen load is secured in a much more efficient manner than could be achieved by manipulation of the dead bee, and the bee can be liberated, thus avoiding unnecessary damage to the colony.

Two methods have been used for the subsequent preparation of the pollen for examination. The first method is substantially that used in the preparation of pollen samples from peat, and the writer is indebted to Dr H. Godwin for suggesting its use. The pollen sample is treated in the tube with 1 ml. of glacial acetic acid containing 5 % sulphuric acid and

heated on a boiling water-bath for 20–30 min. The dark liquid, after being centrifuged, is removed with a fine pipette, and the residual 'acetolysed' pollen washed twice on the centrifuge with distilled water. The pollen remains as a brownish wet mud which is melted in a small piece of glycerine jelly (safranin stain), a small drop removed with a pipette and mounted under a thin cover-slip.

All the material collected during 1941–4 was prepared for determination by this method, a type collection of pollen grains from some 200 species of plants (including horticultural varieties of crop plants and ornamentals) being built up simultaneously. I am not emphasizing any particular advantages in the method over any other—it just happened to be the first method used. Pollen grains prepared in this way, of course, bear little resemblance to the original material, at least in those species having a thin exine. The whole grain contents along with the cellulosic layers of the intine are removed, leaving only the lignified exine. The shape of the grain is markedly altered in the majority of the species, the walls collapsing along the line of the furrows whose original form is largely obscured. However, beautifully clear permanent mounts (the stain has not faded after 4 years) are obtained and the exine sculpture, which is so important in the determination of species, can easily be examined.

The method, however, has definite disadvantages. First, it is rather long and tedious, and as it has been developed for the difficult process of the separation of pollen from peat, it is not necessary to use such a procedure where the pollen samples are uncontaminated with water-insoluble matter. Secondly, as Dr R. Melville has pointed out to me, by destroying the intine many additional characters of potential value in the separation of the genera and species associated with that layer (sculpture, areas of thickening, form of furrow or pore derived from the protruding intine) are lost. Thirdly, owing to the inevitable manipulative losses, an appreciable quantity of pollen is required to give an adequate mount. This introduces difficulties not only with a small load taken from a bee, but in the collection of type samples from very small flowers with little pollen.

A second simpler method was used during 1945; I am unable, at present, to compare the merits of each method, as I have only examined the few 1945 samples reported in this paper, which provided no difficulties in determination. The acetolysis is omitted, the pollen sample is merely soaked in a drop of melted safranin/glycerine jelly, intimately mixed and a drop mounted as before. In the preparation of type samples the pollen can be shot directly on to the slide from the flower with a needle, and covered with a drop of melted jelly hanging from a cover-slip. With this procedure, the finished mount usually requires a further slight warming, otherwise the grains do not take up the stain and do not expand fully, retaining their fresh elongated shape. The last point is important in achieving standard conditions of treatment, because as a whole bee pollen load is usually much too large to mount in its entirety, it is better to treat it separately in the tube as deposited by the bee and to remove an aliquot, in which case the longer treatment of soaking and staining will cause the grains to take up their fully expanded state. Some workers (Wodehouse, 1935, p. 106) wash the grains on the slide with alcohol to assist adhesion and to remove resinous materials present on the exterior of some grains, e.g. Compositae. It seems to me that this practice has potential dangers in the case of mixtures in that the lighter grains might be differentially floated to the periphery of the mount, with a resultant interference with the uniformity of the sample. It is for this reason and owing to the comparatively large size of a bee pollen load that I have not followed the usual practice, but prefer to put up with the resinous secretions and take an aliquot from a well-mixed sample prepared separately.

The pollen grains are identified by comparison with type samples using a $\frac{1}{12}$ in. oil-immersion lens (N.A. 1·30). As a preliminary guide in the determination of species the colour of the sample recorded at the time of collection, combined with a knowledge of the plants flowering at the time, are fully utilized. Taking a diagonal or zigzag course over the mount, a representative sample of about 1000 grains is counted and the percentage number of grains of each species recorded. Subsamples of 200 grains taken during the counting of the whole sample show that with the major component species, the variation in the percentage of these is so small that a sample of 1000 grains gives reasonably accurate figures for the relative frequencies. In the case of pollens consisting principally or entirely of one species smaller samples are adequate.

3. SPECIES THAT VISIT FRUIT TREES

The species of *Andrena* whose flight period coincides with the flowering of fruit trees during the months of April and May are of especial interest because of their possible value in the cross-fertilization of these crop plants. By reason of their comparatively small numbers in individuals and their tendency to forage only under favourable weather conditions of at least moderate sunshine and absence of wind, *Andrena* is very probably of less importance in this respect than the species of *Bombus* which, in addition to being more numerous in individuals, will fly in rougher weather than even the honey bee will tolerate. Against this, the pollen-carrying apparatus and methods of *Andrena* are better suited to perform the act of pollination as, contrary to *Bombus* and the honey bee, which moisten their pollen loads with nectar or honey and carry them as compact loads on their smooth tibiae, *Andrenae* keep their pollen loads

dry, the grains readily adhering to brushes of hairs on their hind tibiae (scopa) and ventrally on their hind trochanters and coxae (floccus). Previous workers, interested in fruit pollination rather than the ecology of *Andrena*, have drawn attention to the importance of these bees as pollinators. In Britain, Wilson (1933) recorded the species of *Andrena* visiting a wide range of fruit blossoms (tree, bush and ground crops) at Wisley, observations being made of the bees' activity, i.e. whether collecting nectar or pollen. The work reported was limited to observations, no examination of the composition of pollen loads being made. Seven species of *Andrena* were considered to be important pollinators. The Canadian workers Brittain & Newton (1933, 1934) compared the pollen-collecting activity of *Andrena* species with other native bees and the honey bee on apple. The bees were taken on a wide range of plants before flowering of the apple and only on the latter during its blossoming period. The loads were examined and pollen grains identified, but no quantitative figures for species composition were recorded. The native bees (almost exclusively non-British) were compared in regard to their pollen constancy to apple with the honey bee. Further records of species of *Andrena* taken on apple have been published by Brittain (1935), *A. wilkella* Kirb. being the only British species mentioned. Apart from a few papers of which these are examples, the number of studies of pollination by wild bees is very small compared with the huge literature on the same activity of the honey bee. In this section of the paper I am recording the data obtained up to date upon visits to fruit trees.

The flight periods and relative abundance are obviously the first criteria governing the effectiveness of species as fruit pollinators, and as both of these factors depend to a great extent upon the locality, no general list of species can be drawn up. The following remarks are based upon my own experience in the southern half of Bedfordshire. The species of greatest potential value as pollinators, by reason of time of flight and abundance, are *A. armata* (Gmelin), *A. haemorrhoa* (Fab.), *A. varians* (Rossi), *A. pubescens* Oliv., *A. thoracica* (Fab.) (local) and *A. flavipes* Panz. (local). In addition, *A. jacobi* Perk. might be added, but, although an ubiquitous species possibly exceeding any other in total number of individuals, by reason of its habit of digging solitary scattered burrows, the number of individuals in any particular locality is not likely to be great. The same considerations apply to *A. minutula* (Kirb.): this habit makes the study of these two species a tedious undertaking. *A. bicolor* (Fab.) is another likely species of widespread occurrence, but in my experience it resorts to woodlands for preference. There are other often abundant or even ubiquitous species whose utility is dubious as they either fly before the blossoming period, e.g. *A. apicata* Smith, *A. clarkella* (Kirb.),

or just after or covering the tail-end only, e.g. *A. nigroaenea* (Kirb.), *A. barbilabris* (Kirb.) and *A. wilkella* (Kirb.). In the previous work briefly reviewed above, the bees were as a rule taken on fruit blossoms, which, as I have previously stated, is a method likely to give a misleading estimate of the activity of a species. Although it is much more tedious and yields less data, the removal of a bee's pollen load on the return to its burrow is a more satisfactory procedure.

For comparison with the flight periods of the species of *Andrena* dealt with, Fig. 1 shows the approximate blossoming periods during the years 1941–5 in south Bedfordshire of plum, cherry, pear and apple (no distinction having been made between varieties), and the native *Prunus spinosa* and *P. avium*. In some cases, e.g. cherry in 1942 where no records were made, the flowering period can be inferred from that of the wild species which it closely follows, a procedure which is justified by the expected observation that the species of fruit trees blossom in the same order however 'early' or 'late' the year. Broadly speaking, the horticultural species commence blossoming slightly later than their wild 'counterparts' and for a shorter overall period. The zigzag portions of the lines indicate the approximate period of full bloom. On the same chart are shown the flight periods of the species of *Andrena* dealt with, most of the data in this paper having been obtained from *A. varians, haemorrhoa* and *armata*. The lines begin with the date when authenticated burrows were first observed and finish on the dates when foraging was no longer apparent after several hours close observation of the colony sites. A discontinuous commencement of a line means that the species was already in flight before the first observation was made. Each line represents observations upon one colony or locality where burrows were found: an extension of the line after a break represents observations made elsewhere. The dates upon which pollen samples were secured are shown by crosses. The correspondence in each year between flight periods and duration of flowering of the fruit trees is apparent.

Andrena varians (*Rossi*)

Observations were made upon two colonies of this species, as follows:

(*a*) A large colony situated on the bank of a small stream on sandy alluvial soil of reclaimed marshland at Flitwick, the burrows being partly in small groups but mainly scattered over a distance of about 300 yd. and situated about 6 ft. above water-level. On the outskirts of a village there are numerous fruit trees in small orchards within a few hundred yards of the colony. The colony was mixed, burrows of *A. haemorrhoa* and *A. praecox* being present but not so numerous as those of *A. varians*. The last of these two additional species, a well-known oligolectic bee,
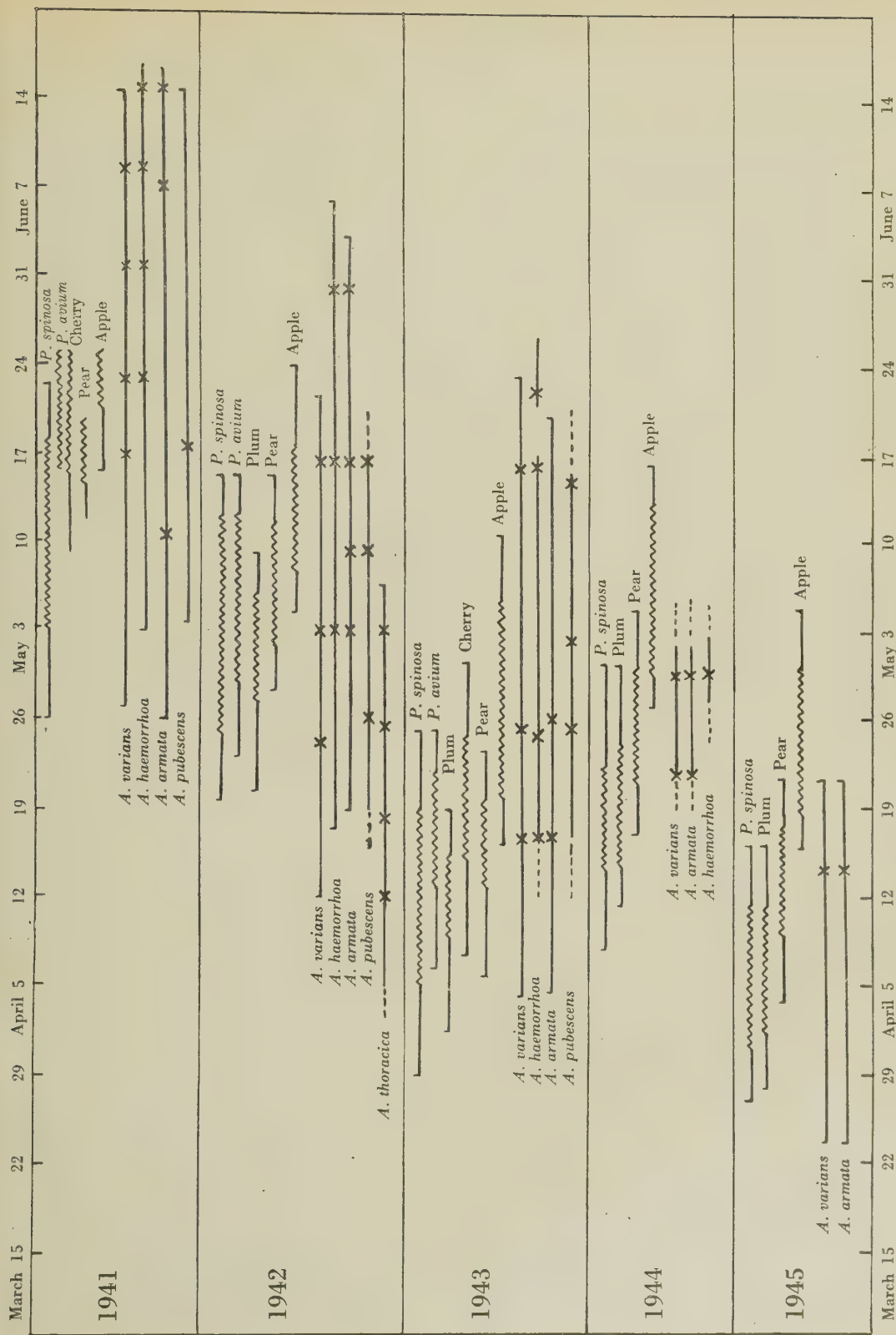
Fig. 1. Flight periods of *Andrena* species and periods of fruit-tree blossoming. For explanation, see text.)

will not be considered, as it only takes pollen from *Salix*.

Observations were made as far as possible at weekly intervals during 1941–3. In 1941 the colony was first discovered on 27 April, excavation of burrows having just started. Although weather conditions were suitable, no foraging was observed on 3 May, while on the 10th lack of sun confined the bees to the neighbourhood of their burrows. Loads were secured from foraging bees on 17 and 22 May and on 1 and 8 June. Active foraging had definitely ceased by 15 June, a flight period of 7 weeks of which only about 27 days, judged upon a subjective basis, were suitable for *Andrena* activity. In 1942—the species was much less numerous—burrow digging had started by 12 April; on the 18th, although the weather was suitable, the bees remained near to their burrows; on the 25th, a little foraging restricted by strong wind; further slight foraging observed on 3 and 17 May, active collecting having ceased by the 24th after a flight period of 5–6 weeks, again about 27 days of which were suitable for foraging. The flight period in the following year lasted for 6 weeks from 3 April until 17 May, with about 24 foraging days possible, loads being secured on 17 April at the height of activity of the species and on 24 April and 16 May. It appears that a period of 1 or 2 weeks elapses between the initiation of burrow digging and foraging with this and other species of *Andrena* even under good weather conditions, but much closer observations are required to confirm this.

(*b*) More limited data were secured in 1944 and 1945 from a small colony, again mixed, including burrows of *A. haemorrhoa*, *A. armata* and *A. pubescens*, situated in short rabbit-grazed turf upon the flat top of a low spur of the Lower Chalk downland at Totternhoe, on the extreme eastern limit of the Bedfordshire-Buckinghamshire plum-growing area. The nearest plum orchard is 200 yd. from the colony. I have no complete record of the duration of the flight period of this species in 1944: in 1945, both sexes were first seen on 24 March, there being no burrows evident. Owing to poor weather conditions at the week-ends pollen loads were not secured before 14 April, all activity having ceased a week later. This gives a flight period of about 4 weeks with some 21 days suitable for foraging; this short period is probably explained by the curtailed blossoming of the plums and by the last week consisting of ideal 'bee weather' of unbroken sunshine and high temperatures.

Analyses of the pollen loads of *A. varians* from the Flitwick colony are given in Table 1, the records from Totternhoe being included for comparison with those of the other species in Tables 3 and 4. The results are expressed as percentage number of grains of each plant species in a representative sample of 1000 grains from each load. To avoid complication, in some cases minor constituents have been omitted from the tables. These are as follows: no. 21 *Sisymbrium alliaria* 2%, no. 24 *Taraxacum* 1%, no. 87 *Anthriscus sylvestris* 2%, no. 88 *Ilex aquifolium* 3%.

It is convenient to give some notes upon the identification of pollen species and explanation of the notation employed in the tables at this stage. Pollen grains of *Prunus* species are readily recognized by the 'thumb-print' striations of the exine, a character shared with a few other genera of the Rosaceae, e.g. *Potentilla*, with which they are not likely to be confused. In the native species *Prunus spinosa* and *P. avium*—which I am unable to distinguish apart—the striations flow directly from pole to pole: I have not come across any grains of *P. spinosa* with whorled striations, the presence of which, according to Allen (1937), enables a separation to be made from *P. avium*. The cultivated varieties of plum—at least those of the commonly grown varieties whose pollen I have examined—are easily distinguished from the native species by the presence of much larger, more globular grains, with in most cases much more strongly developed striations arranged in whorls, although some varieties show a mixture of forms—including abortive grains—approaching those of *P. spinosa*. For this reason it is not possible to report an exact percentage of plum in a mixture, so that I have indicated by a + the presence of plum in those samples containing the characteristic large, whorled grains. I have not attempted to distinguish between horticultural varieties, which may be impossible.

Cultivated varieties of cherry approach more nearly the native species of *Prunus* in form, but are rather larger, and the exine, which sometimes has whorled striations, is thicker. Some varieties are also readily recognized by the abnormally high proportion of abortive grains, which has been taken as a valuable guide when looking for cherry pollen. Because of the difficulties in diagnosis, it is possible that this pollen has been overlooked in some samples. In the loads containing *Prunus* taken at both colonies where no cultivated species has been detected, from the local flora it may be assumed that the only species present is *P. spinosa*. The grains of species of *Pyrus* (apple and pear varieties), although distinct from *Prunus*, are more difficult to separate one from another, and closely resemble those of *Crataegus* and other rosaceous genera. In this and other genera which contain more than one common species, e.g. *Ranunculus*, to avoid an unjustified pretence of accurate determination, I have indicated the probable species, judged by period of flowering or abundance in the neighbourhood, by enclosing the trivial name in brackets, or in the case of cultivated plants the common name, by which they will always be listed, scientific names in general being reserved for native species to avoid complication. Accurate determination of species in some families, e.g. Cruciferae, is often difficult, in which case the most probable

Table 1. *Pollen loads of Andrena varians (percentage number of grains)*

(a) Flitwick, 1941

Date	17 May													22 May								1 June		8 June			
Load no.	20	21	24	25	26	29	30	31	33	34	35	36	37	47	48	49	50	51	52	53	54	67	71	85	86	87	88
Total *Prunus*	90	89	.	80	34	95	8	1	21	1	41	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plum present	+	+	.	+	+	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cherry present	+	+	.	+	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Total *Pyrus*	10	.	2	20	64	5	92	99	79	99	59	100	80	16	100	100	100	81	100	100	100	100	100	.	.	.	.
(Pear)	+	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	.	.	.
(Apple)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Doronicum	.	9	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.
Salix (alba)	.	.	96	.	1	.	.	.	.	.	.	.	.	84	.	.	.	19	.	.	.	.	.	.	.	.	.
Acer (pseudo-platanus)	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	58	42	.
Crataegus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	98	97

(b) Flitwick, 1942

Date	25 April		3 May	17 May	
Load no.	211	212	231	248	249
Total *Prunus*	97	96	8	.	.
Plum present	+	+	+	.	.
Total *Pyrus*	.	.	92	100	100
(Pear)	.	.	+	+?	+?
(Apple)	.	.	.	+?	+?
Ranunculus (ficaria)	2	.	.	.	.
Doronicum	.	4	.	.	.

(c) Flitwick, 1943

Date	17 April																					24 April	
Load no.	366	368	369	370	371	372	373	374	375	376	377	378	379	380	381	382	383	384	385	386	387	399	400
Total *Prunus*	77	tr.	60	2	15	23	.	.	93	.	18	.	100	.	.	.	.	.	1	.	75	.	.
Plum present	.	0	0	0	0	+	.	.	+	+	0	0	0	.	.	.	.	.	.	+	+	.	+
Cherry present	0	0	0	0	0	.	.	.	+	.	0	0	+	.	.	.	.	.	+	+	.	+	+
Total *Pyrus*	17	.	40	93	48	77	100	100	7	98	82	56	.	48	100	100	24	100	99	100	25	95	100
(Pear)	+	.	+	+	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	+	+
(Apple)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Barbarea?	.	.	.	.	.	.	.	.	.	2	.	20	.	.	.	.	.	.	.	.	.	.	.
Cultivated *Brassica*	.	.	.	.	.	.	.	.	.	.	.	15	.	.	.	.	63	.	.	.	.	1	.
Salix (caprea)	.	.	.	5	37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Acer (pseudo-platanus)	.	.	.	.	.	.	.	.	.	.	.	.	.	52	.	.	13	.	.	.	.	.	.
Gooseberry	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Currant	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.

species is given in brackets. The remaining species reported offer no difficulties by comparison with authentic material.

Andrena haemorrhoa (*Fab.*)

Pollen loads of this species were secured during 1941–3 from the mixed colony at Flitwick: the Totternhoe site providing only very scanty data in 1944. The number of pollen loads available for study was much less than in the case of *A. varians*, as, in my experience, unlike the latter, this species is not gregarious, the extent of burrow excavation on any

worn females with large pollen loads having been taken at the end of June even in an 'early' year such as 1945. *Andrena varians* is sometimes seen collecting pollen from *Crataegus*, which starts flowering just before the apples have finished and is much frequented by *Andrena haemorrhoa*.

Table 2 gives the analyses of pollen loads collected by this species at Flitwick in 1941–2. Only three females with pollen were taken at this site in 1943: on 17 April, no. 367 consisting of *Pyrus* (pear) 97 %; *Arabis* 3 %; on 24 April, no. 402 *Acer* (*pseudoplatanus*) 100 %; and no. 426 on 16 May consisting of *Crataegus* 100 %.

Table 2. *Pollen loads of* Andrena haemorrhoa (*percentage number of grains*)

(*a*) Flitwick, 1941

Date ...	22 May				1 June		8 June						15 June	
Load no. ...	57	58	59	60	64	65	89	90	91	92	93	94	104	105
Total *Pyrus* (apple)	.	.	.	54	54	56	.	.	.	.	.	.	.	.
Salix (*alba*)	99	.100	100.	7	18	44	.	.	.	.	.	.	.	.
Acer (*pseudo-platanus*)	.	.	.	14	.	.	.	.	.	.	.	17	.	.
Taraxacum	.	.	.	13	.	.	.	.	.	.	.	.	.	.
Bellis	.	.	.	12	.	.	.	.	.	.	.	.	.	.
Ranunculus (*bulbosus*)	.	.	.	.	28	.	3	.	3	.	.	.	.	.
Crataegus	.	.	.	.	.	.	97	100	81	84	98	84	100	95
Barbarea?	.	.	.	.	.	.	.	.	16	.	.	.	.	.
Brassica	.	.	.	.	.	.	.	.	.	16	2	.	.	.
Quercus	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Anthriscus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	5

(*b*) Flitwick, 1942

Date ...	3 May			17 May		
Load no. ...	232	233	234	250	251	252
Total *Prunus*	73	92	100	.	.	.
Plum present	+	+	0	.	.	.
Cherry present	+	+	+	.	.	.
Total *Pyrus*	27	1	.	100	53	27
(Apple)	?	.	.	+	+	+
(Pear)	?	.	.	.	.	.
Salix (*alba*)	.	7	.	.	43	62
Acer (*pseudo-platanus*)	.	.	.	.	4	2
Quercus	.	.	.	.	.	9

particular site varying from year to year, hence the erratic appearance on the *A. varians* colonies. As it is a much more abundant species than the latter, its habit of digging scattered burrows difficult to find in any numbers, gives quite an incorrect picture of its status in the fruit blossom fauna. I have a number of additional loads taken from both of these species at burrows or on flowers, but as they were taken in districts remote from fruit trees they will not be considered at this stage.

A. haemorrhoa appears slightly later than *A. varians*, but it does not cease activity quite so soon as does the latter after the end of the flowering of *Prunus* and *Pyrus*, foraging being continued on a wide variety of plants until a much later date, very

Andrena armata (*Gmelin*) *and* A. pubescens *Oliv.*

The only data that I have for these two species taken from colonies in the neighbourhood of fruit trees are those from Totternhoe in 1944–5 for *A. armata* given in Tables 3 and 4 and for *A. pubescens* in Table 4. Both of these species fly during the fruit-blossoming period beginning with the flowering of *Prunus spinosa* and extending to that of *Acer*. Fig. 1 shows the flight periods for *Andrena armata* at Whipsnade Heath for the years 1941–3: none of the loads secured contained pollen from fruit trees. A large colony of *A. pubescens* situated on a wide roadside verge, also in the parish of Whipsnade, was observed during these three years. In 1941 the flight period extended from 4 May until 15 June,

while in the following year burrow construction had just started on 19 April and pollen loads were secured on the three ensuing week-ends until activity had practically ceased by 16 May. The flight period in 1943 was very similar in incidence and duration to that of the previous year. As there are no fruit trees within the probable flight range of these species in these two localities, the data obtained will not be dealt with at this stage.

Andrena thoracica (*Fab.*)

The first generation of this species appears too early in the year to cover more than the commencement of the period of blossoming of fruit trees. In 1942 at a compact colony in Warren Wood, Clophill, burrow digging was well under way by 5 April,

There are a large number of fruit trees in small orchards and large bushes of *Prunus spinosa* well within the flight range of the species, which obviously paid no particular attention to these, but collected from a wide range of native plants in the vicinity; no purpose would be served by listing them in this paper.

4. DISCUSSION

A better comparison between *Andrena varians* and *A. haemorrhoa* in their response to fruit-tree blossom could have been made if the data for the latter species from Flitwick had been more extensive. Table 5 gives the genera represented to the extent of 1 % or more of the total number of grains in each load, the number of loads in which each genus is represented

Table 3. *Pollen loads of* Andrena (*percentage number of grains*), *Totternhoe, 1944*

Andrena varians

Date ...	24 April						30 April		
Load no. ...	498	499	500	501	502	503	508	509	510
Total *Prunus*	86	100	100	100	100	99	100	.	50
Plum present	All	All	All	All	+	All	.	.	+
Total *Pyrus* (pear or apple)	.	.	.	.	.	tr.	tr.	100	50
Bellis	13	.	.	.	.	1	.	.	.
Tussilago	1	.	.	.	.	.	.	.	.

Andrena armata

Date ...	22 April		
Load no. ...	495	496	497
Plum	100	100	100

Andrena haemorrhoa

Date ...	30 April	
Load no. ...	506	507
Plum	tr.	2
Fagus	83	89
Aubretia?	4	2
Taraxacum	13	.
Bellis	.	7

pollen loads being secured on 12, 18, 25 April and on 3 May, foraging having practically finished by 10 May. Of the pollen loads secured, only those taken on 25 April and 3 May would be likely, from an inspection of the data on flowering periods in Fig. 1, to contain *Prunus* or *Pyrus*. Seventeen loads were taken on these two dates together, of which only three, collected on 3 May, contained more than insignificant traces of fruit-tree pollen:

No. 225
Pyrus	79 %
Salix (*triandra*)	21 %

No. 226
Prunus (*P. spinosa* and plum)	71 %
Nepeta hederacea	29 %

No. 227
Prunus (*P. spinosa* and cherry?)	100 %

and the number of loads containing more than 50 % of the pollen of each, for the two species. The number of genera, and genera represented, in the pollen loads of these two species are therefore very similar, but it must not be overlooked that a larger number of different genera might have been represented in the loads of *A. haemorrhoa* if the number examined was of the same order as that for *A. varians*. The less frequently represented genera can be omitted from the discussion at this stage, although with some of these, e.g. *Ilex, Bellis, Anthriscus, Ranunculus* and *Doronicum*, their low frequency and content in the loads is without doubt due to the relatively small number of flowers of each available for foraging. The higher representation of *Crataegus* in the loads of *Andrena haemorrhoa* is in accordance with expectation, as this species flies later than *A. varians*.

Differences between the two species in the other major constituents of loads are more marked. *A. varians* shows a more definite preference for collecting the pollen of *Prunus* and *Pyrus* than does *Andrena haemorrhoa*, the proportion of loads containing *Salix* and the quantity of pollen collected, which may be taken as a rough guide to the number of inflorescences visited, both being much lower than by the latter species. Considering only the loads for the two species taken during the fruit-blossoming period, with *Andrena varians*, 44 of the total of 51 loads contain 90 % or more of fruit-tree pollen, only 10 contain more than 5 % of other pollen species,

attractive to this species as sources of pollen, the frequency with which each genus is represented in the loads probably being dependent upon the relative abundance of the flowers of the two crops in a district during the period of overlap of blossoming. Thus apple and pear are much less numerous than plum trees in the Totternhoe district, which explains the high frequency of pure loads of the latter, whereas at Flitwick, where plum, cherry, pear, apple and *Prunus spinosa* occur in quantity, pure loads of *Prunus* rarely appear in the results, more especially as the flowering periods of the forms of *Prunus* overlap to some extent with that of pear.

Table 4. *Pollen loads of* Andrena (*percentage number of grains*), *Totternhoe,* 14 *April* 1945

Andrena varians

Load no. ...	665	666	667	668	669	670	671	672
Total *Prunus*	100	88	.	95	12	95	47	100
Plum present	0	+	.	+	+	All	All	All
Total *Pyrus* (pear)	.	12	100	5	88	5	53	.

Andrena armata

Load no. ...	673	674	675	676	677	678	679	680	681	682
Total *Prunus*	.	.	.	90	86	21	.	.	.	.
Plum present	tr.	.	.	+	+	+	.	.	.	.
Total *Pyrus* (pear)	.	.	.	5	.	.	.	.	.	.
Acer (*pseudo-platanus*)	97	100	100	5	.	29	100	100	100	100
Gooseberry	3	.	.	.	.	.	.	.	.	.
Fagus	.	.	.	.	10	.	.	.	.	.
Senecio vulgaris?	.	.	.	.	3	.	.	.	.	.
Ranunculus (*ficaria*)	.	.	.	.	1	50	.	.	.	.

Andrena pubescens

Load no. ...	683	684	685	686	687	688
Total *Prunus*	1	3	4	9	3	2
Plum present	+	All	All	+	All	All
Total *Pyrus*	.	.	.	.	tr.	.
Taraxacum	99	65	50	11	21	.
A cruciferous sp.	.	32	.	.	.	.
Acer (*pseudo-platanus*)	.	.	26	.	73	98
Ranunculus (*ficaria*)	.	.	20	2	.	.
Lamium	.	.	.	78	.	.
Bellis	.	.	.	.	3	.

Salix being represented in appreciable amounts in 3 of these; while with *Andrena haemorrhoa*, the corresponding figures for the 13 loads are 4 and 9 loads respectively, 9 loads having appreciable amounts up to 100 % of *Salix*. As the apparent or nearest source of *Salix* pollen consisted of only three large trees of *Salix alba*—two of which are more distant from the colony than the nearest fruit trees—it is evident that on the basis of these admittedly limited data, *Andrena haemorrhoa* cannot be considered to have the same high degree of preference for the latter shown by *A. varians*.

The same marked preference for fruit-tree pollen is reflected in the loads of *A. varians* taken at Totternhoe. *Prunus* and *Pyrus* are evidently equally

That cultivated *Prunus* and *Pyrus* are probably equally attractive is demonstrated by the composition of the mixed loads collected when both are in flower, a whole range of percentages of each from low to high being represented, with some indication that the species tends to collect pure loads or at least loads with a high proportion of either, rather than mixtures containing roughly equal proportions of each kind of pollen.

For the reasons previously stated no estimates of relative preference for visits to fruit trees, as shown by pollen loads, by the other early-flying species of *Andrena*, can be made. However, it appears to me reasonable to assume that, regarded as sources of pollen and nectar, the native species of *Pyrus* and the

more abundant species of *Prunus* are not less attractive to these bees than the cultivated forms, which may be regarded as special cases of the same ecosystem. If this is granted, for the purpose of comparing the foraging behaviour of the four species, records of pollen loads containing the native species can be combined with those of loads containing fruit-tree pollen. The following table shows the number of loads containing more than 1 % of *Prunus* or *Pyrus* pollen, together with the number of these containing more than 50 % of either in the whole of the material I have from a number of localities:

	Total no. of loads	Containing *Prunus*	Containing more than 50 % *Prunus*	Containing *Pyrus*	Containing more than 50 % *Pyrus*
Andrena varians	81	45	30	55	40
A. haemorrhoa	41	4	3	10	6
A. armata	43	21	20	1	0
A. pubescens	42	23	4	5	2

From these results it is likely that *Andrena varians* has a more marked preference for fruit-tree pollens than have the other three species, and will show a higher degree of constancy in the foraging behaviour of individuals.

The propensities of *A. varians* and *A. haemorrhoa* for collecting mixed loads of fruit-tree pollens demonstrated above have some practical importance in the cross-fertilization of these crop plants. If an individual bee will fly from one species to another in the course of one foraging trip it is just as likely to visit a number of different varieties of the same 'species' of fruit tree during one flight. The behaviour of these species in this respect can be contrasted with that reported for the honey bee. The pollen constancy of the honey bee, i.e. habit of individual bees of restricting their visits to one species of plant at a time and upon successive flights, has been emphasized by a number of American workers, among whom may be mentioned Philp & Vansell (1932) in their study of the pollination of deciduous fruits, and by Parker (1926), who observed pollen constancy to a variety of flowers. Recently, in England, Butler, Jeffree & Kalmus (1943) have reported extreme examples of constancy, in which marked honey bees were observed to restrict their foraging to very small areas of *Epilobium* and *Echinops* for several successive days. On the other hand, Brittain & Newton (1933, 1934) found that the honey bee does not show the high degree of pollen constancy claimed by some workers for this species, although it is much more constant than the species of *Andrena* studied by these workers in its visits to fruit blossoms. It is probable that, amongst the species of *Andrena*, *A. varians* is of considerable value as a pollinator of fruit trees in localities in which it is abundant, for the following reasons: (a) it shows a marked preference for the massed flowers of fruit trees collectively, (b) individuals

certainly fly from one tree to another in the course of a foraging trip, and (c) alternative available sources of pollen, while made use of, are not so important as counter-attractions as with other species of *Andrena*.

To leave the subject of fruit pollination, it is quite evident even from the limited data presented in this paper that species of *Andrena* do not necessarily forage on all the species or even upon the most abundant species available in the district at any one time. Obviously, the larger the number of loads secured the greater is the probability of any particular available pollen species being found as a constituent. But if foraging by the common species of *Andrena* at present under discussion were quite indiscriminate, one would expect to find the pollen of abundant flowers represented in a proportion of the loads, which has been found not to be the case. For example, during the months of May 1941 and April 1943, when long series of loads of *A. varians* and *A. haemorrhoa* were taken at Flitwick, abundant alternative sources of pollen were as follows:

(1) A large field adjacent to the field in which the colony was situated was full of *Taraxacum* in flower. (Represented in two loads, no. 24 *Andrena varians* (1 %) and no. 60 *A. haemorrhoa* (13 %).)

(2) A large expanse of *Ulex* on the opposite side of the colony to that of the orchards. (Not represented, but in my experience very few species of *Andrena* take pollen from this plant.)

(3) *Sisymbrium alliaria* was abundant between the colony and the orchards. (In no. 21 *Andrena varians* (2 %).) The males of *A. varians* were often numerous on this plant.

(4) A large patch of turnip in flower during April 1943 lying in the direct line of flight from the colony to the orchards, presumed to have been visited only twice by *A. varians* (no. 378 and no. 399 containing 15 and 1 % of this pollen respectively).

The comparative infrequency with which these abundant or showy flowers were visited is all the more surprising when compared with the higher incidence and proportion of *Acer* pollen in the loads, as a prolonged and repeated search of the district located only two trees of sycamore (*A. pseudoplatanus*) as the presumptive sources, both of which are distant several hundred yards from the colony.

A further illustration of apparent selection of pollen sources and of the comparative foraging behaviour of the three species *Andrena varians*, *A. armata* and *A. pubescens* is provided by the analyses of the loads taken at Totternhoe on 14 April 1945

(Table 4), when small but comparable numbers of 8, 10 and 6 loads respectively were taken from bees returning to their burrows on a site no more than 30 × 10 yd. in extent. At the time the plum blossom in numerous small orchards, the nearest of which is some 200 yd. from the colony, was nearly over, petal fall being nearly complete. The flora in the immediate vicinity of the colony was poor, limited to a little *Prunus spinosa* with a negligible ground flora; more distantly were a large number of trees of beech (*Fagus*)—none of which incidentally was seen in flower, with scattered trees of sycamore farther away towards the foot of the hill sloping towards the orchards upon which the colony was situated. In spite of the near termination of flowering of the plums, *Andrena varians* managed to find abundant sources of pollen and ignored or failed to find the closer rich supply of pollen and nectar

probably have included some containing this pollen. However, in both localities plum and *Prunus* pollen generally was that most frequently collected. It would appear that when once a supply of pollen has been located by this species, return journeys to the same source or others in the immediate neighbourhood are made, with the building up of a habit, until the source is exhausted, this being the behaviour characteristic of species whose individuals show a high degree of pollen constancy. Behaviour of this type can therefore be interpreted in this way as due to the psychological property of rapid habit acquisition. Alternatively, it may be due to a hereditary response to the flowers of plants with which the species has lived in association for long periods during which the vegetation has become stabilized, which I am inclined to hold is the more likely explanation in this particular case. Otherwise, again

Table 5. *Summary of data from Flitwick*

	Andrena varians (55 loads)			*Andrena haemorrhoa* (23 loads)	
Genus	No. of loads in which represented	No. of loads with > 50 %	Genus	No. of loads in which represented	No. of loads with > 50 %
Pyrus	47	35	*Pyrus*	9	6
Prunus	25	12	*Salix*	9	4
Salix	5	1	*Crataegus*	9	9
Doronicum	4	1	*Acer*	5	1
Barbarea?	4	0	*Prunus*	3	3
Acer	3	3	*Ranunculus*	3	0
Crataegus	3	2	*Brassica*	2	0
Brassica	2	0	*Quercus*	2	0
Ribes	2	0	*Anthriscus*	1	0
Anthriscus	1	0	*Arabis*	1	0
Ilex	1	0	*Barbarea?*	1	0
Ranunculus	1	0	*Bellis*	1	0
Sisymbrium	1	0	*Taraxacum*	1	0
Taraxacum	1	0			

provided by the sycamores. *A. armata*, while also foraging on plum, on this occasion, showed a definite preference for sycamore, and in addition, one of the females found somewhere a beech tree in flower. The loads of the third species, *A. pubescens*, all contained plum or *Prunus* pollen as minor constituents, sycamore was well represented, the most frequent constituent *Taraxacum* being the favourite source of pollen of this species and which it probably located in good supply in the grassed-down plum orchards and adjoining meadows.

Without attempting to attach too much significance to limited data from one locality, the following considerations may serve to indicate some of the questions which arise from analyses of pollen loads and in what direction further research is likely to lead to fruitful results. Dealing with *Andrena varians*, the data obtained at Flitwick showed that occasional visits to *Acer* for pollen may be made, and a longer series of loads from Totternhoe would

reverting to the Flitwick data, if habit were a major determining factor, a higher proportion of fixations of habit of individual females upon *Salix*—demonstrated by a higher proportion of pure loads of the pollen of this genus—would have been expected than actually obtained. As the adults of the two species *Andrena varians* and *A. armata* emerge at about the same time (see Fig. 1), the early foraging of the latter species in 1945 was no doubt predominantly upon *Prunus*, but on the date upon which the loads under discussion were taken, unlike *Andrena varians*, a definite switch had been made by *A. armata* to the *Acer* which had just started to flower, indicating adaptability to a new situation in the environment. The foraging behaviour of *Andrena pubescens* illustrated by these and other (unpublished) analyses is typical of what would be described as a polylectic species, is qualitatively different from species with the behaviour of *A. varians* and must evidently be interpreted upon a different basis.

This raises the question as to whether *A. varians* should be regarded, upon existing terminology, as a polylectic species. Applying the term in the sense that this bee takes pollen from a considerable number of the limited spring-flowering species (see Table 5) the answer is 'yes'. The same may be said of *A. haemorrhoa*. But the analyses reported have shown that there is good reason to suppose that these two species differ quantitatively in the relative attention paid in foraging to the different species of a similar qualitative range of pollen sources. On the other hand, both species, more especially *A. varians*, exhibit a marked tendency to collect predominantly from one or two species of closely related plants. Of the two terms proposed by Clements & Long (1923) to describe foraging behaviour, that of monodrome constancy is obviously inapplicable to either species of bee in view of the considerable proportion of mixed loads collected. To establish strictly a case of polydrome constancy it would be necessary to analyse the successive loads of individual bees. Restricting the term polylectic to describe the behaviour of the individual bee, conversely, the high proportion of pure loads collected by *A. varians* rules out this application of the term.

The descriptive terms available are therefore inadequate even for the broadest classification of behaviour systems and do not enable the necessary clear distinction to be drawn between the range of pollen plants visited by a bee species and the number of species visited by individuals on each foraging trip. Over and above a floristic analysis of species visited, to enable a comparison of the foraging behaviour of species of *Andrena* or other genus of bee to be made, it may be possible, upon the basis of a large number of analyses of loads, to formulate indices of frequency descriptive of these two distinct aspects of foraging behaviour, which would be useful in assessing the adaptability of different species.

5. SUMMARY

1. A technique for the examination of individual pollen loads collected by bees of the genus *Andrena* is described and its application in the study of the foraging behaviour of these insects is illustrated and discussed.

2. Particular attention is given to the species which fly during the fruit-blossoming period. Of the several species listed which fly at this time, observations of the flight periods of *A. varians, haemorrhoa, armata* and *pubescens* in relation to the flowering of cultivated and native forms of *Prunus* and *Pyrus* in the years 1941–5 are given.

3. Quantitative analyses of the pollen species present in the loads of these four species of *Andrena* taken from colonies in the neighbourhood of fruit trees are reported and compared.

4. The results show that *A. varians* has a definite preference for fruit-tree pollen and is therefore likely to be of some value as a pollinator of plum, cherry, pear and apple in those districts where it is to be found. *A. haemorrhoa, armata* and *pubescens*, although frequently taking the pollen of these crop plants and of native *Prunus*—in pure or mixed loads —do not show the same high degree of preference and pollen constancy.

5. Emphasis is laid upon the differences shown, and the selection that is made, by the different species in the flowers visited for pollen. The significance of these facts in the wider interpretation of the ecology of *Andrena* species as shown by bee-flower relationships is discussed.

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THE COYPU (*MYOCASTOR COYPUS*) IN GREAT BRITAIN

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(With Plates 1 and 2 and 6 Figures in the Text)

CONTENTS

1. INTRODUCTION

Myocastor coypus (Molina), commonly known as the coypu or nutria, the latter being its commercial name, is a large semi-aquatic South American rodent, about the size of an otter, which has been introduced into Great Britain and bred in captivity in order to market its valuable pelt. Some of the first to be farmed in this country arrived by air transport about 1929 (Williams, 1934), since when at least 49 nutria farms have been established. The majority of these were in the southern and south-eastern counties of England, with a few in the north and west, and two in Scotland. Since the beginning of the war in 1939 all these farms appear to have been discontinued.

On account of the semi-aquatic habit of the animals, water is absolutely essential for rearing them successfully, and so farms have been established near natural water supplies. Various methods of penning have been recommended (Williams, 1934; Carill-Worsley, 1932, 1935), which are efficient up to a certain point in preventing their escape. A very suitable method includes the enclosure of a stretch of a stream with wire netting, though here the danger of escape arises, especially when the stream is in flood. A number of escapes have been reported since the introduction of the animal into Great Britain, and several colonies have established themselves in the wild state, particularly in Norfolk. As the coypu is a potentially destructive rodent some alarm has been felt, as it is well known that introduced animals and plants may increase in numbers to a dangerous degree when there are no natural factors to keep them under control. The Norfolk War Agricultural Executive Committee therefore decided to organize trapping campaigns in an effort to eliminate their local infestations. The Bureau of Animal Population was given the opportunity, through the courtesy of Capt. H. W. Palmer, Pests Officer of the Norfolk W.A.E.C., of making some

ecological study of the coypu. I was able to visit the area during the second trapping campaign, in June 1943, and the third, in March 1944; and in April 1944 undertook with the help of J. S. Watson a survey of the Norfolk area as a whole, in order to determine the extent and density of the infestation. I wish to record my thanks to Capt. Palmer and members of his staff for help given during my visits to Norfolk and for records which they obtained for me; to Mr E. A. Ellis, Norwich Castle Museum, for information and help with contacts; to Mr P. E. T. Carill-Worsley for much useful information; to the Land Pests Branch of the Ministry of Agriculture and Fisheries for supplying records of nutria fur farms and of escapes, for the country as a whole; to Miss J. Lambert, Westfield College, London, for her photographs of Surlingham Broad, Norfolk; and to Mr Charles Elton for advice and criticism. The expenses of this investigation were defrayed by the Agricultural Research Council.

2. GENERAL CHARACTERS

The type form *Myocastor c. coypus* (Molina) is a native of Chile, the subspecies *M. c. bonariensis* (Geoffroy) inhabits North Argentina, Uruguay, Paraguay and South Brazil, and *M. c. santaecruzae* (Hollister) the south coast of Argentina (Allen, 1942). Osgood (1943) describes two other subspecies, *M. c. popelairi* Wesmael, an exceedingly large and dark-coloured form inhabiting south-eastern Bolivia, and *M. c. melanops* Osgood, a dark form found in brackish water on Chiloe Island, southern Chile. According to Allen the length of the body and head of a full-grown adult coypu is about 25 in. (64 cm.) and the tail 17·5 in. (45 cm.); they may weigh up to 50 lb. (22,680 g.) (Larrison, 1943, p. 5), but this is rather exceptional. The coypu has a scaly tail, round in section, rather like that of a rat, webbed hind feet, small round ears, large orange-coloured incisor teeth

and the female has the unusual arrangement of dorsally situated mammae, from which the young can be suckled while she is swimming. The pelage consists of a short dense silky brownish grey under-coat covered by a thinner coat of longer coarse glossy yellow-brown guard hairs, which grow through it. These coarse hairs are pulled out when the pelt is prepared for the market. The coypu is extremely docile in captivity and can be easily tamed. The flesh is edible. (Pl. 1, photos. 1, 2.)

3. EXTERNAL PARASITES

Although a thorough examination was made of the 16 coypus caught during the second trapping campaign in Norfolk for external parasites such as fleas and lice, none were found. Since then, however, two lice and a tick have been taken by Mr E. A. Ellis from a young coypu caught near Norwich. The lice, one male and one female, are of considerable interest. They have been identified as specimens of *Pitrufquenia coypus* Marelli (Freeman, 1946). This species belongs to an entirely South American family, the Gyropidae, and so far has only been recorded from its type locality, a single coypu farm at Pintrufquen in the province of Concepcion, Chile. This is rather surprising as several comprehensive accounts of the coypu living in both America and Europe, have been written. The tick, identified by Mr E. Browning, British Museum (Natural History), is a nymph of *Ixodes ricinus* (L.) the 'sheep tick' which readily attaches itself to warm-blooded animals.

4. HABITAT AND FOOD

(a) South America

Their natural habitat in S. America is among swamps and marshes and along the margins of rivers and lakes. They also inhabit the coastal waters and estuaries of Chile and are apparently just as much at home in salt as in fresh water. Osgood (1943), however, suggests that the coypus living in brackish water are a separate subspecies, *Myocastor coypus melanops* Osgood. They are ordinarily vegetarians, feeding upon the aquatic and semi-aquatic vegetation of their habitat, but where they live along the coast, burrowing in the forests which border the shore, they also feed upon shellfish (Parry, 1939). They burrow into the banks of rivers and streams and also make tunnels through the dense thickets of reeds among which they live.

(b) Great Britain

It is not surprising that the coypus have found the great reed-beds and marshes of Norfolk an ideal habitat (Pl. 2, photos. 3, 4). They have also established themselves along the rivers where the banks are fringed by reeds and sedges or trees which provide them with food and cover. The marshland vegetation of the infested areas consists in the main of reeds (*Phragmites communis*) and reed meadow-grass (*Glyceria maxima*) with reed-mace (*Typha latifolia* and *T. angustifolia*) the latter only abundant locally, and sedges (*Carex riparia, C. acutiformis, C. paniculata*). In the summer there is also abundant aquatic vegetation in the rivers and streams such as the water parsnip (*Sium erectum*), Canadian water-weed (*Elodea canadensis*), water-milfoil (*Myriophyllum spicatum*) and arrowhead (*Sagittaria sagittifolia*). An examination of ten coypu stomachs revealed an entirely vegetable diet, but the contents were too finely divided to be recognizable in detail. So far there has been no evidence that molluscs, either salt or fresh water, are eaten by feral coypus in this country.

Two interesting cases of the effect of the feeding activities of the coypu are given on the authority of Mr E. A. Ellis. One is of the complete disappearance of an area of reed-mace (*Typha latifolia*) about 20 by 60 ft. and of some smaller patches, and the other of the reduction of the rare plant cowbane or water hemlock (*Cicuta virosa*) which was fairly common round the margins of Surlingham Broad in 1934, to two plants in 1945. The writer has seen some patches of the new shoots of *Glyceria maxima* which appeared to have been cropped by coypus.

Although the barking of trees is one of their characteristic occupations in captivity, they do not do this to any very noticeable extent in the wild.

5. BURROWS AND NESTS

The burrowing activity, at any rate in those infestations examined, was not at all extensive. The burrows were 8–9 in. (20–23 cm. approx.) in diameter and extended into the bank for about 4 ft. (122 cm.) often with an opening at both ends. The entrance towards the river is usually about the water level. Some of the burrows were under the roots of trees which had been exposed along the bank of the river or stream.

The only nests that have so far been found were made of reeds and sedges built up into large piles somewhat after the fashion of a swan's nest. These were built on the land among the marsh vegetation and close to the water's edge. Four very young coypus, about 5 in. in body length, were caught near to one of these nests during the Norfolk W.A.E.C.'s first trapping campaign in February–March, 1943. The young are very precocious. In captivity they have been seen to come out of their nests within a few hours of birth and within 24 hours to be swimming in the water and feeding on vegetable food. They themselves soon begin burrowing or use the burrows of 'rats', though if the burrow is inhabited they may be killed by the occupying 'rat' (Maurice, 1931).

Vereshchagin (1941) refers to the brown rat (*Rattus norvegicus* Exrl.) as being the chief biological competitor of the coypu in Georgia, U.S.S.R., as they both eat the same food plants, and he points out that

it may also kill young coypus. Among other predators mentioned are the weasel (*Mustela nivalis*), probably the otter (*Lutra lutra*) and various predatory birds—owls, harriers and buzzards.

6. DETECTION

Coypus are fairly easy to detect by the runways made in the vegetation alongside the river or dyke at the point of emergence from the water. The bank is worn down to a saucer-like depression about 8 in. in diameter and the vegetation is trampled down into obvious tracks. The track is often of a very characteristic semicircular form, as though the animal came out on to the bank at one point and then went back into the river a couple of feet or so away. Another useful indication of their presence is provided by the short lengths of vegetation which they cut off and which remain in the runway or float about near the bank. These may be bitten off rhizomes and new shoots of reeds, or longer reeds etc. cut into short lengths. Occasionally their faeces may be found on the landing places or floating in the water. These are 2·5–5·0 cm. long and about 1 cm. wide, cylindrical, slightly curved, with longitudinal striations, and are pointed at both ends. It must be pointed out that the otter makes very similar tracks through the vegetation; but this animal's presence can usually be distinguished by traces of a meal such as fishbones and scales, frogs' skins and empty mollusc shells, which it leaves on the bank. The presence of water-fowl may also make the detection of coypus more difficult. During the summer when the vegetation is dense it becomes very difficult to trace them, therefore surveys should be made when the vegetation has died down in the winter months.

7. DAMAGE

It has been feared that like the muskrat (*Ondatra zibethica* (L.)), the coypus would undermine the banks of rivers and ditches by their burrowing activities, thereby causing a considerable amount of damage and destruction. So far, however, little damage of this kind has been reported to or seen by the writer, though there is always the danger that it might occur should the number of wild coypus increase sufficiently. Burrowing is not necessary for nest building.

Three instances of economic loss due to coypus have been recorded from Norfolk. During the winter of 1942–3, they raided allotments and gardens near the River Yare, completely devouring a number of the green vegetables, showing a decided preference for cabbage. Larrison (1943) states that they are the cause of similar depredation in vegetable gardens near the Sammamish River, Washington, U.S.A. In December 1944 coypus in Norfolk caused considerable damage by eating the roots of a crop of sugar-beet which had been planted along the edge of the river bank, and in November 1945 they were reported eating a crop of sugar-beet at Wroxham, Norfolk. Larrison also quotes Wire (no. ref.) as saying '...we do not consider them a valuable fur animal as they do considerable damage by boring at dikes and levees, doing more harm even than muskrats or beaver....We do not feel that they are desirable animals to have in this state [Oregon] and would be glad to get rid of them.' Maurice (1931) states that in Argentina coypus became pests when at certain times of the year the marshes in which they lived became flooded, with the result that they invaded the cultivated land around the flooded area in order to obtain food and to escape from drowning. Larrison (1943) intimates that they are still a great agricultural pest in Argentina.

They trample down and generally make a mess of marsh vegetation. This has become noticeable in parts of the reed-swamps in Norfolk where they have been established for some time. The complete disappearance of patches of the reed-mace (*Typha latifolia*) due to the feeding activities of coypus has already been mentioned (p. 23). Some people maintain that in this respect it is a useful animal as it prunes and keeps down the vegetation in the dykes and waterways of the reed-swamps!

In the U.S.S.R., where they have been introduced for commercial exploitation, Vereshchagin (1941) in an account of the ecology of coypus introduced into the marshy areas of Georgia, states that during one period of high density they levelled the herbaceous cover of sedge and reed-mace over quite large areas, by eating the young shoots during the spring and in the summer and autumn the tender parts near the root. Among the main food plants of the coypu in south Russia are *Typha angustifolia*, *Sparganium*, *Phragmites communis*, *Glyceria aquatica*, *Carex vesicaria* and *C. riparia*, which are all components of reed-swamp or marsh vegetation in this country. Other plants common to both British and Russian marshes and lakes, which according to Vereshchagin are eaten to a lesser extent but are part of the coypus' normal diet, are *Hydrocharis*, *Scirpus lacustris*, *S. maritimus*, *Cladium mariscus*, *Nuphar*, *Nymphaea* and *Nasturtium officinale*. *Cladium mariscus* is one of the rarer marsh plants of this country and is a scientifically interesting component of the vegetation in the Broads and Fens (Conway, 1942). Vereshchagin also states that coypus are reported to have eaten maize and aubergines in the fields near water.

8. TRAPPING METHODS

Trapping campaigns were carried out by the Norfolk W.A.E.C. with 4 in. gin-traps which were set in the runways of the coypus often just at the edge of the bank where the animals came out of the water. This method was found to be quite successful. It is also said to be quite easy to catch them in box-traps baited with bread.

Photo. E. M. O. Laurie

Photo. 1. Young male coypu (*Myocastor coypus*), weight 793 g. (no. 12, Table 3), caught in a trap near the River Yare, Norfolk, June 1943.

Photo. E. M. O. Laurie

Photo. 2. Adult female coypu (*Myocastor coypus*), weight 4706 g. (no. 15, Table 3), caught in a trap near the River Yare, Norfolk, June 1943.

Photo. J. Lambert

Photo. 3. Part of Surlingham Broad, Norfolk, a habitat of the coypu, showing typical reed-swamp vegetation of *Glyceria* with taller shoots of *Phragmites* and *Typha latifolia.*

Photo. 4. Part of *Phragmites* fringe bordering a channel of Surlingham Broad, a typical habitat of the coypu.

9. DISTRIBUTION AND NUMBERS

(a) General

As has already been stated the coypu is a native of South America. It ranges southwards from the valleys of central Chile at about 33° S. lat. to the straits of Magellan and eastward across Argentina to where in search of food. 'Suddenly a mysterious malady fell on them from which they quickly perished becoming almost extinct' (Allen, 1942). The export of the fur is now under government control.

As a result of the farming of coypus in Washington and Oregon, U.S.A., feral coypus are now
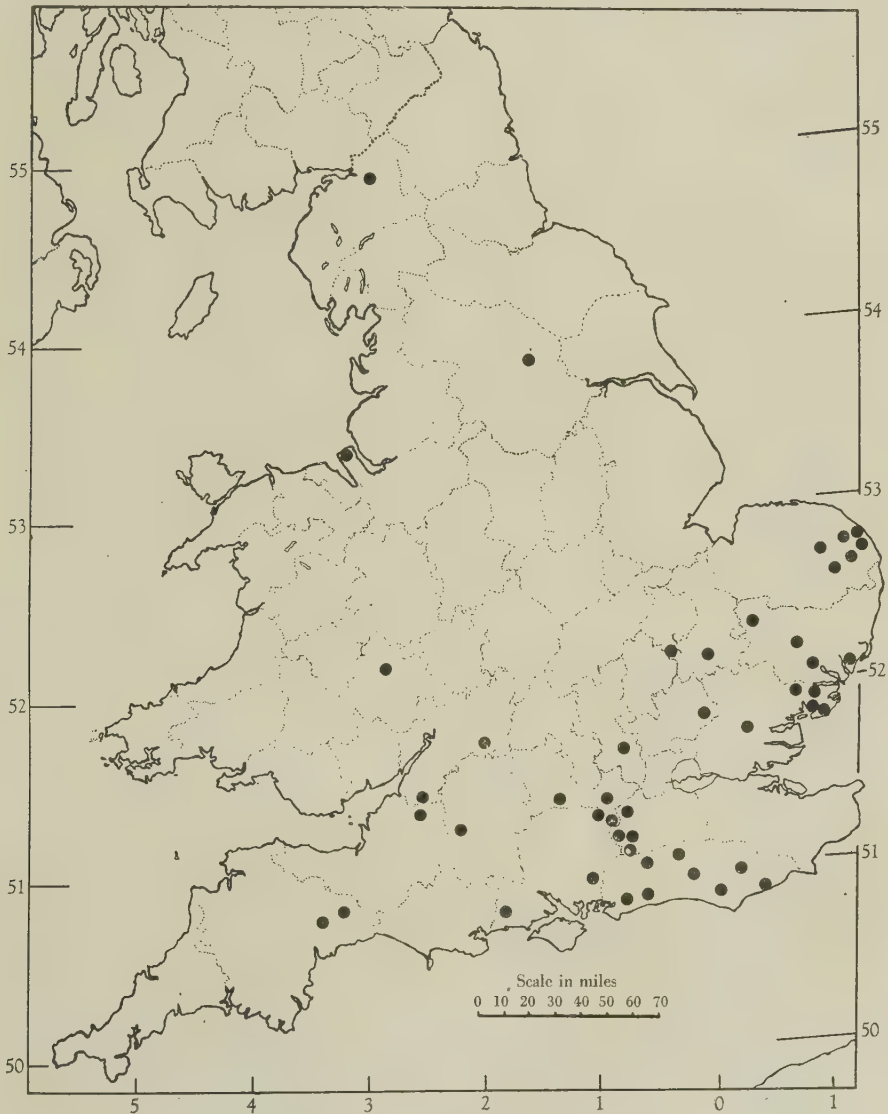
Fig. 1. Distribution of coypu (*Myocastor coypus*) fur farms in England, 1932–9 (approx.).

the extreme south of Brazil, Paraguay and Uruguay. At the beginning of last century, when their fur came into great demand for the making of felt hats, the number of coypus in Paraguay and Argentina became so reduced that the Argentine dictator, Rosas, prohibited the hunting of them. The result was that they multiplied exceedingly and swarmed every-

apparently quite widely distributed in the Pacific North-west (Larrison, 1943). Holdom (1944) gives some account of the occurrence of wild coypus in the general area of Vancouver and New Westminster, British Columbia, noting that there are various fur farms in this area from which they have no doubt escaped.

Table I. *Localities from which coypus* (Myocastor coypus) *have been reported*

1932–5

Warnham, nr. Horsham	Sussex, 1932, 1933
Tiverton	Devonshire, 1933
Ringwood	Hampshire, 1934
Walresley	Huntingdonshire, 1934
Auchinroath, nr. Rothes	Morayshire, 1934
Horsham-Rudgwick	Sussex, 1935
Whiligh	Sussex, 1935

1936–9

Alresford	Essex, 1936, 1937
Confluence of Vyrnwy and Severn rivers	Montgomeryshire, 1936
Farnham	Surrey, 1936
Elstead	Surrey, 1936, 1937
Petworth	Sussex, 1936
Rudgwick	Sussex, 1936
Warnford Mill, River Arun	Sussex, 1936
Wokingham	Berkshire, 1937
Winkfield	Berkshire, 1937
Swallowfield	Berkshire, 1937
Moreton, Wirral	Cheshire, 1937
Tiverton	Devonshire, 1937
Ardleigh	Essex, 1937
Chelmsford	Essex, 1937
Southminster	Essex, 1937
Hawley	North Hampshire, 1937
Aldershot	North Hampshire, 1937
Farnborough	North Hampshire, 1937, 1938
East Carleton	Norfolk, 1937, 1939
Honing	Norfolk, 1937
Camberly	Surrey, 1937
Cobham	Surrey, 1937
Old Place Brook (flows into River Ouse)	Sussex, 1937
Cirencester	Gloucestershire, 1938
Mattingley	North Hampshire, 1938
Lewes-Hailsham	Sussex, 1938
Bray	Berkshire, 1939
Aylesbury-Wendover	Buckinghamshire, 1939
Marsh, nr. Kimble	Buckinghamshire, 1939
Sherfield-on-Loddon	Hampshire, 1939
Weston, River Wensum	Norfolk, 1939
Horsham	Sussex, 1939

1940–3

Chester	Cheshire, 1940
Southampton	Hampshire, 1941
River Wensum	Norfolk, 1941, 1942, 1943
River Tas	Norfolk, 1941, 1942, 1943
River Yare	Norfolk, 1942, 1943
Wheatfen Marsh, nr. Surlingham	Norfolk, 1942, 1943
Wolverhampton	Staffordshire, 1942
River Blackwater	Hampshire, 1942
North Curry	Somerset, 1942
Stoke St Gregory	Somerset, 1942, 1943
Turvey	Bedfordshire, 1943
Dorney, nr. Slough	Buckinghamshire, 1941, 1942, 1943
Aldershot	North Hampshire, 1943
Pensford	Somerset, 1943
Tattingstone Place, nr. Ipswich	Suffolk, 1943
Uckfield	Sussex, 1943

1944–5

Dorney, nr. Slough	Buckinghamshire, 1944, 1945
Dovercourt	Essex, 1944
Gorleston, Yarmouth	Norfolk, 1944
Rivers Yare, Wensum and Tas	Norfolk, 1944, 1945
Binfield	Berkshire, 1945
Northwold	Norfolk, 1945
Wroxham, River Bure	Norfolk, 1945

The coypu was introduced into France, where it is known under the name of 'ragondin', at least as early as 1882 (Bourdelle, 1939). Here again they have escaped from farms and have successfully established themselves in the wild, mainly in central France.

Coypus have been introduced into the U.S.S.R. on a large scale since 1926 with great success (Vinogradov & Argiropulo, 1941). Here they have been deliberately let loose in marshy areas in the hope that they would become acclimatized and breed freely in the wild. Many were liberated in the

press and to the Ministry of Agriculture and Fisheries. These were mainly from Hampshire, Sussex, Surrey and Norfolk, counties in which a number of farms were established (Fig. 1). These escapes have usually been reported as being shot or recaptured but occasionally they remained at large. The reports from the various localities have been grouped together for periods of 4 years, from 1932–5, 1936–9, 1940–3, and the 2-year period 1944–5 (Table 1) and their distribution shown in Figs. 2–3.

The farms (Fig. 1) were mostly in lowland country where rivers and streams are slow running with
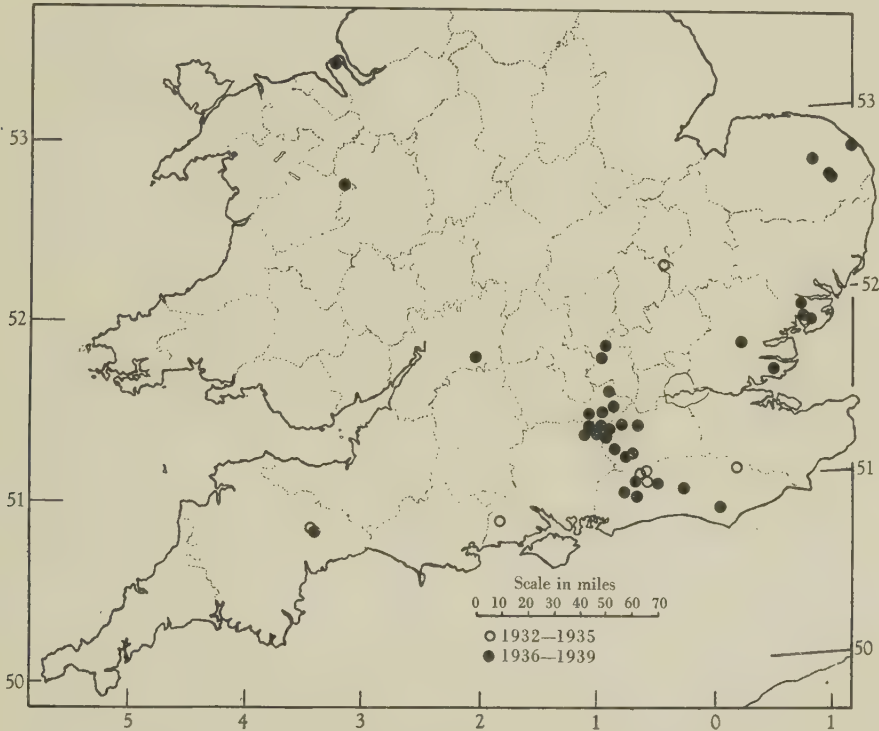
Fig. 2. Localities in England and Wales from which escaped coypus (*Myocastor coypus*) were reported from 1932 to 1939.

plains near to the rivers Kura, Rion and Kuban in the Transcaucasus (Bobrinskii, Kuznetzov & Kuzyakin, 1944). Vereshchagin (1941) gives an excellent account of the establishment of coypus in the marshy areas of West Georgia, U.S.S.R.

Coypus have also been bred extensively in captivity in Germany and to a lesser extent in Austria, Norway and Belgium.

(b) Great Britain

Since 1932, three years after their introduction into this country as a commercial animal (Williams, 1934), various escapes have been reported in the

muddy banks. The swiftly running streams and rivers of more hilly country, which have hard rocky beds and often far less vegetation, are less suitable. A number of coypu farms were established by the owners of estates through which a stream or river ran, and were not conducted on a very large scale. Some larger farms were, however, established in at least Norfolk, Sussex and Hampshire. One of the Norfolk farms supported a minimum of a hundred animals at one time and was said to be one of the largest in Britain. These farms were quite successful.

Coypus have also been bred in Scotland but the writer only knows of two farms, one at Auchinroath, near Rothes, Morayshire, and one at Perth.

It will be seen that there have been quite a large number of escapes (from 50 % of the farms which were known to be in existence), though at the present time (1945) coypus are only known to be established in any numbers in Norfolk and in Buckinghamshire, in which latter county they have colonized a sewage farm near Slough. The record at Binfield, Berks., was only of a single coypu. In Norfolk the coypus

Table 2. *The weight increments of four young coypus* (Myocastor coypus) *kept in the Zoological Gardens, London. Born on 2 April* 1945

Weight in g.

Date 1945	Male no. 1	Female no. 2	Female no. 3	Female no. 4
12 April	370	315	415	385
19 ,,	470	375	505	475
28 ,,	590	405	610	580
3 May	530 (dead)	425	625	615
17 ,,	—	820	980	950
31 ,,	—	1065	1240	1175
14 June	—	(Died)	1415	1280

complained of the damage caused by coypus eating green vegetables in gardens and allotments near the River Yare. As a result the W.A.E.C. started trapping along the banks of the Yare in the Cringleford-Keswick neighbourhood with the result that 40 coypus were caught. In June 1943 a second campaign lasting ten days was carried out along more or less the same area and 16 coypus were caught. They were next reported farther up the Yare between Cringleford and Bawburgh and in January–February 1944, 42 coypus were trapped along this part of the river. From the survey made in April 1944 the limit of their range up the Yare appeared to be Marlingford, less than a couple of miles upstream from Bawburgh. This area between Keswick and Marlingford appeared to be fairly well trapped out except for a residue in the neighbourhood of Earlham Hall, where many of the traps were stolen.

The coypus have also colonized about 9 miles of the River Wensum between Drayton and Lenwade, though not in such large numbers, and rather discontinuously. Only 8 were trapped here in March

Table 3. *Details of coypus recorded by the writer, from the rivers Yare and Tas. The body weight of pregnant females is the net weight without embryos*

River	Date	No.	Sex	Weight lb.	Weight oz.	Weight g.	Body length cm.	Tail length cm.	Condition of reproductive organs
Yare	8 June 1943	1	Female	12	12	5783	58·0	31·0	Pregnant, 9 embryos, wt. 198.45 g.
,,	,,	2	,,	4	8	2041	37·0	25·4	Corpora lutea
,,	,,	3	,,	4	6	1984	42·3·	24·4	Corpora lutea and in oestrus
,,	,,	4	,,	4	4	1927	39·6	24·4	,,
,,	,,	5	,,	4	2	1871	37·2	22·4	,,
,,	,,	6	Male	5	8	2494	40·9	22·4	Fecund
,,	,,	7	,,	5	6	2438	45·0	25·0	,,
,,	,,	8	,,	3	2	1417	35·7	22·4	Probably fecund
,,	9 June 1943	9	,,	10	13	4904	47·5	30·3	Fecund*
,,	,,	10	,,	6	3	2806	42·2	29·0	,,
,,	11 June 1943	11	,,	5	1	2296	39·6	30·4	,,
,,	15 June 1943	12	,,	1	12	793	27·6	19·8	Not fecund†
,,	,,	13	Female	1	13	822	25·4	19·8	No corpora lutea
,,	,,	14	,,	1	12	793	27·6	19·8	,, *
,,	,,	15	,,	10	6	4706	51·5	34·3	Corpora lutea and spots in uterus
,,	16 June 1943	16	Male	1	13	822	25·4	19·8	Not fecund
,,	7 March 1944	17	Female	9	8	3975	48·3	33·0	Pregnant, 5 embryos, wt. 325 g.‡
Tas	9 April 1944	18	Male	14	0	6350	—	—	Fecund

* Skull kept.   † Skin kept.   ‡ Skull and skin kept in the Bureau of Animal Population.

have colonized a total of about 40 miles along the rivers Yare, Wensum and Tas. These infestations have probably arisen from escapes from three fur farms, one at Weston near the Wensum, one at East Carleton between the Yare and the Tas, and one at Brundall near the lower reaches of the Yare (Fig. 4). All three farms have now been given up.

The first reports of the Norfolk infestation received by the Norfolk W.A.E.C. came from the Cringleford Parish Council in February 1943, which

1944 and this area is again under control. There are also a few colonies along the River Tas which are supposed to be under the control of local gamekeepers.

In April 1944 it was obvious that coypus were fairly numerous in the marshland around Surlingham, Wheatfen and Rockland Broads. Since then the W.A.E.C. have trapped 66 coypus from this area during April, May and June 1944. In October 1944 a report was received by Mr E. A. Ellis, Norwich
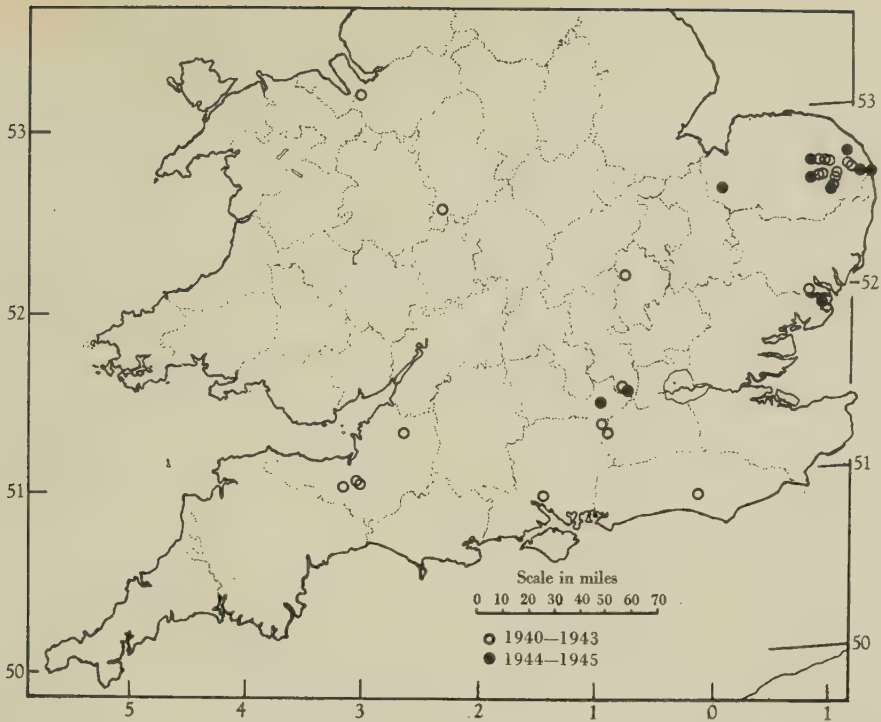
Fig. 3. Localities in England from which escaped coypus (*Myocastor coypus*) were reported from 1940 to 1945.
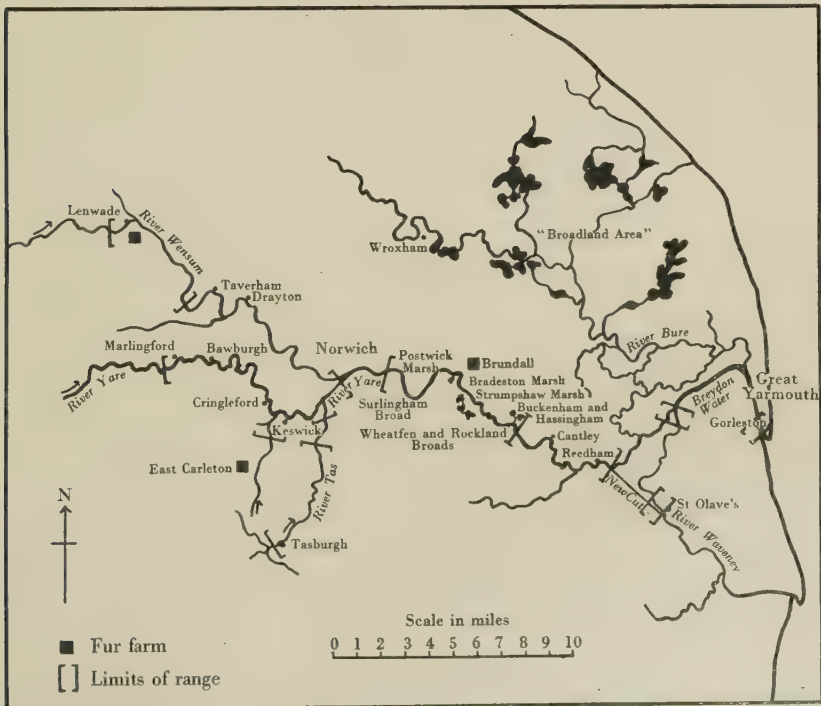

Fig. 4. Range of coypus (*Myocastor coypus*) along the rivers Wensum, Yare and Tas, Norfolk. Range above Hassingham from survey made in April 1944; below Hassingham from reports during the winter 1944–5. A few were reported from Wroxham, River Bure, in November 1945.

Castle Museum, of one killed at Gorleston, Great Yarmouth, in the estuary of the River Yare. No others have been reported from here but it is of interest to remember that in South America, their native country, they are as much at home in salt water as in fresh, though it is suggested that a separate subspecies is involved (Osgood, 1943). There have been various reports during the winter of 1944–5, of coypus occurring for the first time along the lower reaches of the River Yare. They are

none have been reported from the Broads, but in November 1945, reports were received that they had been found in small numbers at Wroxham, on the River Bure, where they had been seen eating sugar-beet.

In January 1945 a coypu was shot at Northwold on the River Wissey, Norfolk. This is some 24 miles, as the crow flies, south-west from the Yare and Wensum infestations. As far as I have been able to ascertain they have never been farmed in this
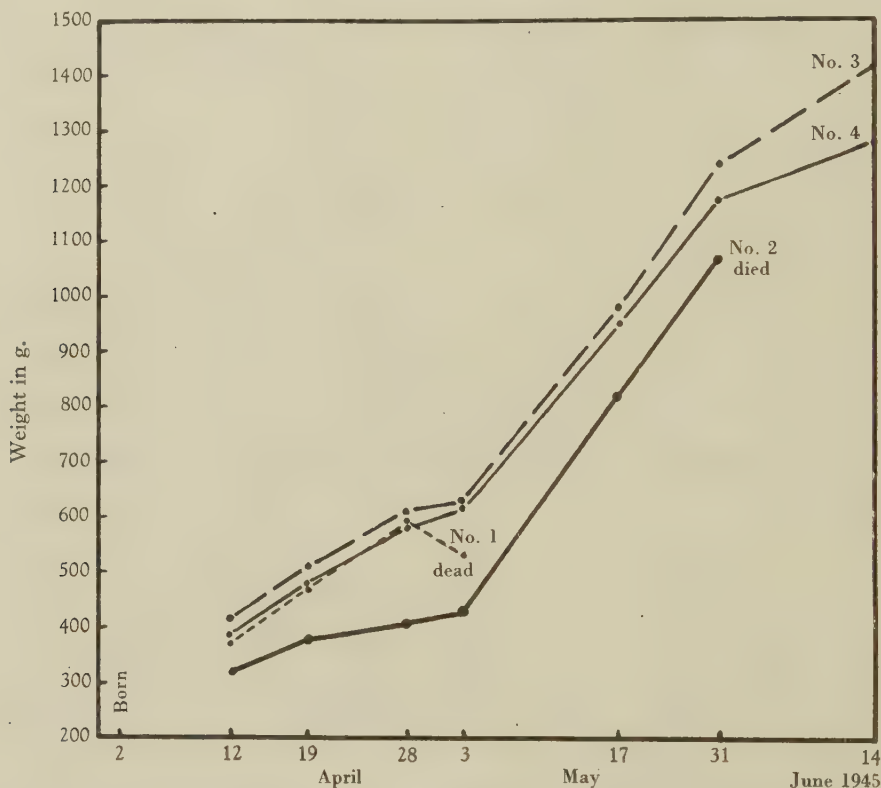
Fig. 5. The weight increment of four coypus (*Myocastor coypus*) kept in the Zoological Gardens, London. No. 1 was a male, and nos. 2, 3 and 4 females.

certainly moving down from the Hassingham area. In January–February 1945 three were killed on the opposite side of the river from Cantley, two along the river at Reedham, one in the marsh between the New Cut and the River Waveney near to St Olave's and one in the marsh where the Rivers Yare and Waveney run into Breydon Water. From an examination of these localities made in February 1945 it did not appear as though they were established in any numbers, at any rate not below Cantley, but it was obvious that there was a very real danger that they might invade the Waveney and Bure rivers and so get via the latter into the main Broads. So far

neighbourhood, and there are no signs of any more along this part of the river.

To sum up: between February 1943 and June 1944, the Norfolk W.A.E.C. trapped 172 coypus, and in June 1945 a further 21 were caught in the Rockland area, making a total of 193. Owing to the shortage of labour no trapping was done between June 1944 and June 1945.

10. REPRODUCTION

In their native country, according to Cabrera & Yepes (1940), the gestation period lasts from 127 to 132 days, there being two litters a year and some-

Table 4. *Coypus trapped at Surlingham and Rockland Broads, Norfolk, by the W.A.E.C., and recorded by them. The weight of pregnant females includes the weight of embryos*

Date 1944	No.	Sex	Weight lb.	Weight g.	Condition of reproductive organs
18 April	1	Female	16	7257	Pregnant
	2	,,	14	6350	
	3	Male	12	5443	
	4	,,	10	4536	
	5	,,	10	4536	
	6	,,	9	4082	
	7	,,	9	4082	
	8	Female	10	4536	Pregnant
	9	,,	8	3628	
	10	,,	8	3628	
	11	,,	8	3628	
	12	,,	8	3628	
	13	Male	13	5896	
	14	,,	3	1360	
	15	,,	3	1360	
29 April	16	Female	20	9072	Pregnant
	17	,,	12	5443	
	18	,,	6	2721	
	19	Male	6	2721	
	20	,,	6	2721	
	21	,,	6	2721	
	22	,,	6	2721	
6 May	23	Female	16	7257	Pregnant
	24	,,	14	6350	Pregnant
	25	,,	14	6350	Pregnant
	26	,,	12	5443	Pregnant
	27	,,	12	5443	
	28	,,	8	3628	
	29	Male	15	6804	
	30	,,	8	3628	
	31	,,	6	2721	
	32	,,	2	907	
	33	,,	2	907	
	34	,,	2	907	
	35	,,	2	907	
13 May	36	Female	14	6350	Pregnant
	37	,,	12	5443	Pregnant
	38	,,	8	3628	
	39	Male	11	4989	
	40	,,	10	4536	
	41	,,	8	3628	
	42	,,	8	3628	
13–20 May	43	Male	7	3175	
	44	Female	23	10432	Pregnant
	45	,,	16	7257	Pregnant
	46	,,	8	3628	
	47	Male	12	5443	
	48	,,	10	4536	
	49	,,	9	4082	
6 June	50	Female	18	8164	Pregnant
	51	,,	10	4536	
	52	,,	9	4082	
	53	Male	14	6350	
	54	,,	10	4536	
	55	,,	10	4536	
17 June	56	Female	10	4356	Pregnant
	57	Male	18	8164	
	58	,,	14	6350	
	59	,,	12	5443	
24 June	60	Female	17	7711	Pregnant
	61	,,	15	6804	
	62	,,	8	3628	
	63	,,	6	2721	
	64	Male	7	3175	
	65	,,	6	2721	
	66	,,	6	2721	

times five in 2 years. At each pregnancy the female has from two to eleven young, five being about the average. Breeding continues throughout the year. The young are born furred and with their eyes open and soon begin to feed upon the same diet as their parents, as has already been mentioned (p. 23).

These figures agree with those given for coypus bred in captivity in Great Britain and France, except that Carill-Worsley (1935) and Williams (1934) give the gestation period as 120 days for coypus breeding in Britain. According to Maurice (1931) fecundity may be attained when they are about 4–5 months

Through the courtesy of Dr G. M. Vevers a series of records was kept of the increase in weight of four coypus born and reared in the London Zoological Gardens. Unfortunately two of the young coypus died and it was only possible to obtain records of the other two up to an age of 10 weeks and 3 days (Table 2, Fig. 5). These showed a gain of a little over 400 g. per month, which agrees with the figures given by Maurice (1931) quoted above.

Flower (1931) gives the average length of life of 20 coypus kept in the London Zoological Gardens as 4 years and 8 months, the maximum being 5 years
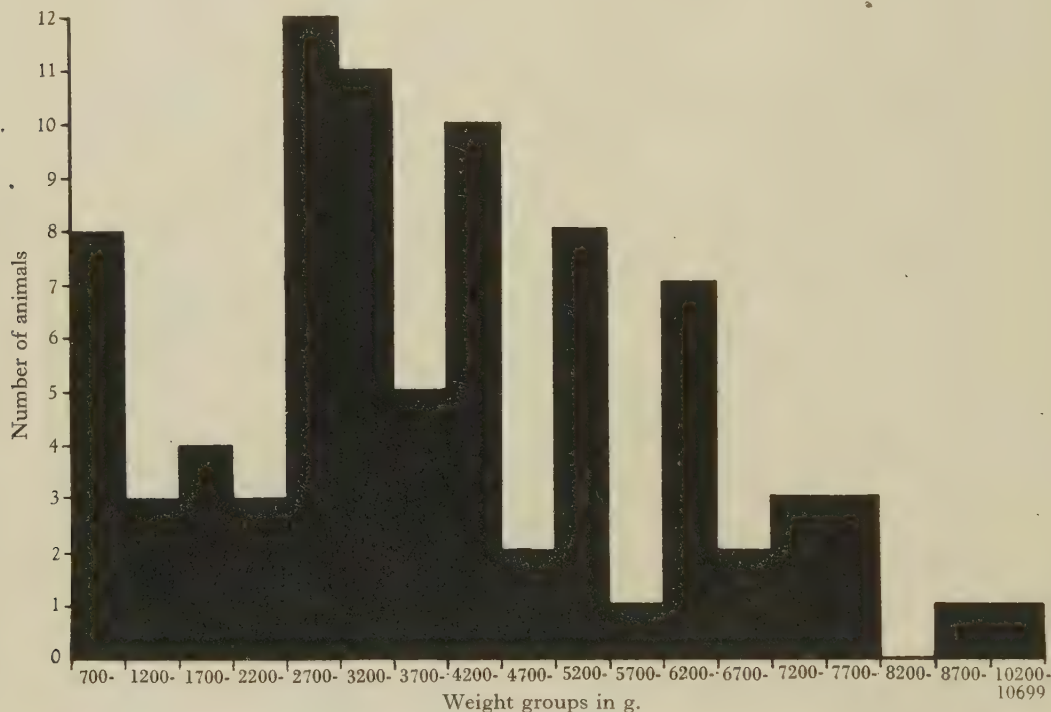

Fig. 6. Weight distribution of 24 coypus (*Myocastor coypus*) caught in Norfolk, June 1943–June 1944.

old. The females sometimes give birth to their first litter when they are 8 or 9 months old, but 10, 12 or even 15 months are more usual ages. Maurice also found that the average weight at birth (of 50 coypus) was 200 g., that for the first year there was an average gain of 400 g. per month, and that thereafter growth continued with less regularity. There were, however, indications of seasonal changes, a slowing down in winter followed by a recovery in spring and a slight slowing down in July–August. Growth also appears to be more rapid at puberty, say between 4 and 6 months and in general the male grows a little more quickly than the female. Considerable deviations from the average may be caused by variations in temperature and food.

11 months and 2 days. Chalmers Mitchell (1911) gives 12 years as the maximum length of life and 2½ years as the average of 39 coypus kept in zoos in England, Maurice (1931) gives 10 years as the normal length of life for coypus in captivity in France, and Vereschagin (1941) gives 8 years as a rough figure for longevity in the U.S.S.R.

Through the kind co-operation of the Norfolk W.A.E.C. it has been possible to obtain records of some of the coypus caught during their trapping campaigns. The sex, weight (to the nearest pound), condition of the reproductive organs, whether fecund or pregnant, and in some cases the number of embryos and length of body and tail were recorded. The presence of corpora lutea in the ovary of the

females and of a fairly large number of sperms in the cauda epididymidis of the testes of the males, were taken as the criteria of fecundity. No detailed records were obtainable for the first 40 coypus trapped in February–March 1943 but such details as have been ascertained are as follows: 25 were large enough for their skins to be considered of market-able value, which would make them at least 6 lb. (2·7 kg.) or more body weight; 11 of these were large, estimated to be above 10 lb. (4·5 kg.), the largest being a male weighing about 20 lb. (9 kg.).

More precise details have been recorded for the sixteen coypus caught between 7 and 16 June 1943 (Table 3). These included both young and adult animals, and one pregnant female containing nine embryos. In March 1944, a pregnant female was shot at Lakenham on the River Yare, and a male said to weigh 30 lb. (the largest specimen trapped by the Norfolk W.A.E.C.) was caught on the Wensum (one of eight trapped there). Data for the 66 coypus trapped on the Rockland and Surlingham marshes near Norwich were obtained through the Norfolk W.A.E.C.: 30 of these were females, 14 of these being pregnant, and 36 males, their weights ranging from 2 to 18 lb. (Table 4). The weight distribution of the 84 coypus caught between June 1943 and June 1944 (Tables 3, 4), is shown graphically in Fig. 6. (I have also a record of a pregnant female with 8 embryos which was killed at Wheatfen Broad, Norfolk, in November 1944.)

It appears from this material that under wild conditions in Norfolk the coypu continues to breed throughout the year, as when it is bred in captivity in this country. A high proportion of fecund females were found to be pregnant, 16/37 (Tables 3, 4). The approximate weight and age at which fecundity is reached appears to be about the same as that inti-mated by Maurice (see p. 32) that is 1800–2200 g. (4·5 lb.) about 4–5 months, and the number of embryos 5, 8 and 9 in three females, is up to and above the average of 5.

11. SUMMARY

1. The coypu (*Myocastor coypus*), a South American rodent, has been bred in Great Britain for its valuable pelt since about 1929. Most of the fur farms were in the southern and south-eastern counties of England and were given up in 1939 on account of the war.

2. There are records of a number of escapes from these farms and wild colonies of coypus are estab-lished at least in parts of east Norfolk, and on the Dorney sewage farm near Slough, Buckingham-shire.

3. The Norfolk War Agricultural Executive Committee is carrying out a trapping campaign with 4 in. gin traps, and has already caught 193 coypus between February 1943 and June 1945.

4. The coypus live along the banks of rivers and streams which they may burrow into, and in marshy land close to open stretches of water.

5. The vegetation in these habitats consists of various aquatic plants, particularly sedges (*Carex* spp.) and reeds (*Phragmites communis*), which provide cover as well as food. Stomach examinations of 10 specimens showed an entirely vegetable diet.

6. The weight of 84 coypus caught in Norfolk ranged from 793 g. (1 lb. 12 oz.) to 8164 g. (18 lb.) excluding weights of pregnant females plus em-bryos. The heaviest coypu was a pregnant female plus embryos which weighed 10432 g. (23 lb.). The heaviest male weighed 8164 g. (18 lb.).

7. There does not appear to be any marked difference in the reproductive rates of coypus living wild in Great Britain and those bred in captivity in Great Britain, or in South America, France or Russia. Breeding continues throughout the year, fecundity in both sexes being reached at a weight of about 1800–2200 g. (4–5 lb.), about 5 months old. In captivity the gestation period lasts for about 120–130 days, the average number of young per litter is 5 and there are 2 litters a year, sometimes 5 in two years. Three pregnant females which were examined by the writer had 5, 8 and 9 embryos respectively.

8. Two specimens of the louse *Pintrufquenia coypus* were obtained from a coypu caught near Norwich. So far it appears to have only been re-corded from its type locality in Chile. This is the first record for Great Britain.

9. Some account is given of the recorded habitat and food of the coypu in South America and its general distribution apart from Great Britain.

10. In some parts of the world the coypu is regarded as a pest. In Great Britain it has been the cause of some damage to crops and a little to river banks. More serious damage is being done to the reed-swamp vegetation which it feeds upon and tramples down.

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THE FOOD OF THE SHAG (*PHALACROCORAX ARISTOTELIS*) IN THE CLYDE SEA AREA

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(With 1 Figure in the Text)

1. INTRODUCTION

During the four-year period 1936–9 the stomachs of 81 shags (*Phalacrocorax aristotelis*) shot on the south-west coast of Scotland were examined by the writers. Three of these were obtained in the Sound of Jura (mid-Argyll); all the others were shot in the Clyde sea area, mainly round the Cumbrae Islands.

The original object of the investigation was to find whether the diet showed marked seasonal variation. While in the case of a few of the more commonly encountered food organisms a superficial examination of the data seemed to indicate the existence of such variation, more critical study showed that the fishing locality is the most important factor, far outweighing other local influences such as weather, state of the tide, etc. Further, it was found that in the present sample apparent seasonal variation in the diet could be accounted for by the fact that many birds were sometimes collected during a single visit to one particular spot.

Steven (1933) discusses records of the stomach contents of a large number of shags and cormorants shot on the coast of Cornwall, but the method of collection employed in his work did not permit a study of the birds concerned before shooting. In the present investigation—though the number of specimens is small when compared with Steven's series—an attempt was made to gain information relating to the bird and its behaviour just before shooting. Many of the birds were obtained at the large shag roost on the Little Cumbrae and in these instances the data were of necessity incomplete, but in the case of almost all the specimens from other localities the records included the date, fishing locality, weather notes, state of tide, observed behaviour during the fishing period, whether the bird was single or in company with others, etc. In all cases the state of the reproductive organs was noted and it was found that most of the birds concerned were immature, as in spring, when the majority were shot, adults are scarce in the Clyde sea area—possibly on account of breeding habits.

As mentioned above, the nature of the fishing ground—which depends mainly on the type of sea floor—was found to be by far the most important factor influencing the diet of the shag. For the sake of brevity the results will be discussed with reference to this factor only.

2. METHODS

The birds were opened as soon as possible after death and the stomachs removed, split down one side, and placed in formalin to arrest the rapid digestive process. Any fish found in the highly distensible oesophagus were removed at the same time. The great capacity of the oesophagus may be gauged from the fact that a specimen of the closely allied cormorant (*Phalacrocorax carbo*) which was shot on the wing off the Great Cumbrae was found to have in its gullet a complete flounder (*Pleuronectes flesus* L.) 1 ft. in length.

The material was prepared for examination as follows: whole fish, large fragments and easily recognizable objects were picked out, measured and rinsed in water, the washings being returned to the main mass of material. The latter was gently agitated in several changes of water, the supernatant fluid—containing only flocculent mucus and unrecognizable debris—being decanted slowly after settling had taken place. The remaining material consisted chiefly of otoliths, fish bones, scraps of flesh, nematodes and small miscellaneous objects, and was examined in large green photographic developing dishes. The medium tint of this background rendered conspicuous many small white otoliths which would have been overlooked in an ordinary porcelain dish.

In cases where fish fragments were present, tails were always more numerous than heads, so that counts of fish were based on this observation. The persistence of tail fragments after the digestion of the heads is probably to be accounted for by the bird's habit of swallowing the fish head foremost. If the stomach is full, fish may remain wholly or partly in the oesophagus and the hind portions escape for some time the action of the gastric juice.

In many cases food other than fish was found in the stomach. Much of this—small amphipods, isopods and molluscs—was clearly derived from the fish. It was impossible in such cases to make a sharp distinction between shag food and fish food, but for practical purposes it was considered unlikely that the bird would capture deliberately any animal smaller

than the shrimp, *Crangon*. This standard has been used throughout.

The stomach almost invariably contained large numbers of nematodes, some of which were doubtless derived from the fish.

3. FEEDING HABITS

When a shag on the water is about to begin fishing, it repeatedly dips its head under the surface, a habit also seen in captive penguins before feeding. The appearance suggests that the bird is looking for fish. When diving, the bird springs clear of the water surface and enters head first, making very little splash. Towards the end of the fishing period, when loaded with food, it sometimes slides under water in a 'seal dive' without the preliminary leap.

On favourable ground a shag may complete its meal in one long series of dives. On other occasions, after a run of a few dives, it may fly off and begin again elsewhere. Ten complete series of dives were observed and timed with a stop-watch, and in this sample the number of dives varied from 7 to 29 per series, the mean being 15. Sometimes a bird may be seen to dive repeatedly within one small area, but more frequently it fishes in a zigzag line, finally turning and traversing back over the same ground to its starting point. Such a course may often extend well over a mile. At the end of the fishing period the shag again dips its head under water several times, but in this instance only to scoop water over the back. After a period of preening and washing accompanied by vigorous flapping of the half-opened wings, the bird either settles down on the water, flies off or, after an interval, resumes fishing.

The keeper of the diving birds in the London Zoological Gardens states that when captive shags are feeding on small living fish in a large tank they may swallow several without coming to the surface. Large fish, however, are brought to the surface before being eaten. Our observations in the field are in agreement with this statement, as we have frequently seen a shag rise to the surface with the beak empty but gaping slightly, while a transitory bulge in the neck showed that a fish had been swallowed under water. Large fish are brought to the surface in order that they may be manipulated into a suitable position for swallowing.

When swimming under water the shag holds the wings closely pressed to the sides. The legs are angled outward and the feet, widely separated, beat simultaneously. While surface fish form a large part of the diet, our records show that many bottom-dwelling forms are eaten in large numbers and in this connexion it is interesting to note that the shag may swim so close to the bottom as to turn up a trail of sand in its wake. Further evidence of feeding actually on the bottom (and of the habit of swallowing small prey under water) is given by the fact that pebbles were found in four stomachs, shells in fourteen, an *Echinocyamus* test in one, coralline alga in one and large quantities of muddy sand in one.

The shag is a highly efficient fisher. On one occasion we saw a bird bring up six medium-sized fish (thought to be wrasses) in seven dives, and on another three smallish flatfish were brought up in the course of four dives. Newbigin & Elmhirst (1931) mention a case where a shag was watched fishing for $1\frac{1}{2}$ hr., after which it was shot. On examination the stomach was found to contain seven sticklebacks, forty-one gobies, two wrasses and one saithe—a total of fifty-one fishes. In the London Zoological Gardens a shag is allowed a normal diet of three herrings per day; but in nature the quantity of food consumed is usually much greater and it is well known that shags and cormorants frequently gorge till they cannot rise from the water. If alarmed in this state they may have to regurgitate fish before they can take off.

With regard to the ten series of timed dives mentioned above, the following facts may be noted: the total periods covered by individual series varied from 6 min. to almost 23 min., the mean being just over 13 min. It was found that the duration of the dives bore no relationship to the depth of the water nor to the preceding and subsequent resting periods. In all cases the time spent under water was considerably greater than that spent resting at the surface, the ratios in individual cases ranging from 1 : 2 to 1 : 5. The mean ratio resting-time : diving-time was 1 : 3. It was found that the duration of the actual dives varied very considerably. Taking a mean for the entire sample of 155 observed dives, the figure of 40 sec. was obtained, but the longest dives varied in individual cases from only 40 sec. to 1 min. 40 sec., and the shortest dives from 5 to 35 sec. In the case of resting periods the mean was 15 sec., but individual maxima varied from 15 to 40 sec. and individual minima from 5 to 10 sec. In all the above cases the figures have been corrected to the nearest 5 sec.

4. LOCALITIES AND GENERAL DATA

The material was collected in ten different localities. Shags shot at the roost are placed in one group and the remainder are arranged according to the nature of the sea floor over which they had been fishing. The relevant data are as follows:

Group 1. Forty-seven shags obtained at the roost, Little Cumbrae (Table 1)

The roosting place of most of the birds of the Cumbrae area is on the rocky west coast of the Little Cumbrae. In the evening several hundred shags from widely separated localities congregate there. In this group general data are scanty as only a few of the birds were watched fishing. According to Mr R.

Table 1. *Stomach contents of forty-seven shags shot at the roosting place, Little Cumbrae*

Food	No. of specimens	No. of stomachs concerned
Annelida:		
Nephthys sp.indet.	1	(1)
Mollusca:		
Loligo sp.indet.	1	(1)
Crustacea:		
Pandalus montagui Leach	1	(1)
Leander serratus (Pennant)	5	(3)
Leander squilla (L.)	1	(1)
Crangon vulgaris L.	18	(7)
Carcinus maenas (Pennant)	2	(1)
Fish:		
Clupea sprattus L.	29	(1)
Clupea sp.indet.	23	(2)
Spinachia vulgaris (L.)	1	(1)
Syngnathus acus L.	11	(6)
Ammodytes sp.indet.	283	(12)
Gadus pollachius L.	8	(4)
Gadus virens L.	1	(1)
Gadus sp.indet.	7	(5)
Pholis gunnellus (L.)	44	(14)
Zoarces viviparus (L.)	1	(1)
Callionymus lyra L.	19	(3)
Callionymus sp.indet.	6	(3)
Gobius ruthensparri Euphrasen	4	(2)
Cottus scorpius L.	2	(2)
Cottus sp.indet.	10	(5)
Agonus cataphractus (L.)	3	(2)
Labrus bergylta Ascanius	1	(1)
Ctenolabrus rupestris (L.)	18	(5)
Otoliths:		
Syngnathus acus L.	13	(2)
Ammodytes sp.indet.	2663	(17)
Gadus minutus L.	13	(3)
Gadus pollachius L. and virens L.	322	(30)
Callionymus sp.indet.	43	(7)
? Gobiidae or Pleuronectidae	146	(17)
Cottus sp.indet.	46	(12)
Ctenolabrus rupestris (L.)	59	(8)
Unidentifiable	543	(21)
Totals:		
Annelida	1	(1)
Mollusca	1	(1)
Crustacea	27	(12)
Fish	471	(40)
Otoliths	3848	(43)

Feathers were present in twenty-two stomachs, pebbles in four, coal in one, coralline alga in one, polychaete jaws in six, an *Echinocyamus* test in one, small Crustacea (fish-food) in four, shells in thirteen, fish eggs in five, and recognizable fish debris in various stomachs which contained no whole specimens of the corresponding species namely: *Callionymus* vertebrae in two, *Syngnathus* plates in three, *Ammodytes* debris in one and teeth of Labridae in eleven.

Elmhirst, Director of the Marine Station, Millport (private communication), shags fly to the roost from points as much as 22 miles distant. Obviously this sample is a heterogeneous one, including birds which had fished over many different types of sea floor.

Group 2. Fourteen shags obtained in localities with a rocky or stony sea floor (Table 2)

In this group are included twelve birds shot around Keppel, Great Cumbrae. The coast in this area is rocky, shelving fairly steeply to deep water. Owing to strong tidal currents there are no large accumulations of mud or sand. Also included are one bird from Tomont End, at the north of the Great Cumbrae (where the coast is similar) and one from Port Lunna, a small deep rocky sea loch which forms an arm of Loch Sween, mid-Argyll.

Group 3. Eight shags obtained in localities with a rock, shingle and mud ('mixed') sea floor (Table 3)

The birds in this group were all obtained at Balloch Bay, Great Cumbrae. This large, open bay, which shelves slowly, has a muddy and sandy bottom with belts of stones and rock.

Table 2. *Stomach contents of fourteen shags shot in localities with a rocky sea floor*

Food	No. of specimens	No. of stomachs concerned
Crustacea:		
Leander serratus (Pennant)	1	(1)
Leander squilla (L.)	3	(1)
Crangon vulgaris L.	4	(1)
Carcinus maenas (Pennant)	1	(1)
Maiid crab	1	(1)
Fish:		
Clupea harengus L.	9	(1)
Spinachia vulgaris (L.)	19	(8)
Gadus pollachius L.	13	(5)
Pholis gunnellus (L.)	27	(8)
Callionymus sp.indet.	1	(1)
Gobius ruthensparri Euphrasen	23	(4)
Cottus sp.indet	6	(3)
Ctenolabrus rupestris (L.)	7	(5)
Otoliths:		
Clupea harengus L.	10	(5)
Gadus merlangus L.	1	(1)
Gadus pollachius L. and virens L.	119	(11)
? Gobiidae or Pleuronectidae	7	(1)
Cottus sp.indet.	17	(6)
Unidentifiable	44	(4)
Totals:		
Crustacea	10	(3)
Fish	105	(14)
Otoliths	198	(13)

Feathers were present in seven stomachs, a piece of bracken in one, large polychaete jaws in one, a cephalopod shell in one and teeth of Labridae in two.

Group 4. Twelve shags obtained in localities with a sandy or muddy sea floor (Table 4)

Two birds were collected at Eilean nan Coinean, Sound of Jura, mid-Argyll, a small rocky island surrounded by wide stretches of sandy sea floor. Tidal currents are exceptionally strong in this area. Six shags were shot near Millport Pier which stands in a deep, sheltered bay with a sandy floor over most of its area but containing some small rocky islets. Three were obtained at Fairlie, Ayrshire, where there is an extensive tract of muddy sand, about a mile wide, which is mainly exposed at low water. One shag was shot at Horse Island, near Ardrossan, Ayrshire. This small rocky island rises from a sandy and muddy sea floor.

Detailed records of the individual birds and records of the ten series of timed dives have been deposited at the Marine Station, Millport.

5. OTOLITHS

Considerable numbers of fish otoliths were almost always present in the stomach contents, being recorded from 76 of the 81 birds. Papers by Scott

Table 3. *Stomach contents of eight shags shot in localities with a mixed type of sea floor (rock, shingle and mud)*

Food	No. of specimens	No. of stomachs concerned
Annelida:		
Nephthys caeca (O. F. Müller)	1	(1)
Crustacea:		
Crangon vulgaris L.	16	(2)
Unidentified Caridean	1	(1)
Fish:		
Clupea sp.indet.	10	(2)
Ammodytes sp.indet.	59	(3)
Gadus pollachius L.	1	(1)
Gadus sp.indet.	2	(2)
Pholis gunnellus (L.)	7	(1)
Callionymus lyra L.	1	(1)
Callionymus ? maculatus Raf.	4	(1)
Otoliths:		
Clupea harengus L.	17	(3)
Ammodytes sp.	18	(3)
Gadus pollachius L. and *virens* L.	68	(6)
? Gobiidae and Pleuronectidae	2	(2)
Cottus sp.indet.	9	(2)
Unidentifiable	408	(6)
Totals:		
Annelida	1	(1)
Crustacea	17	(2)
Fish	84	(7)
Otoliths	522	(8)

Feathers were present in five stomachs, pebbles in one, muddy sand in one, shells in one, fish eggs in one, small Crustacea (fish-food) in one and ovigerous females of *Chondracanthus ornatus* (from *Callionymus maculatus*) in one.

(1906) and Frost (1925–30) were used for their identification. The majority were usually found in the saccular part of the stomach adjoining the pylorus.

The numbers of otoliths were usually much greater than could be accounted for by the fish in the stomach and often belonged to species not otherwise represented. A considerable proportion were worn and unidentifiable. It would appear, therefore, that the otoliths persist in the stomach for some time. This is particularly true of the large stout Gadoid otoliths, which frequently occurred in considerable numbers. On account of this probable persistence in the stomach it was not permissible to include otoliths (or fish bones or wrasse tooth plates) in calculating food percentages for given types of sea floor. Though they give useful information about the past diet of individual birds they may have been derived from fish previously eaten in some other area. Examination of faeces from the roost showed that otoliths may be passed rapidly through the gut as complete and undamaged specimens were found (though in small numbers) in this material.

It has been suggested that otoliths may play some part in triturating the food in the stomach in the same manner as stones in the gizzard of a fowl. In view of their small size, however, and of their aggregation in one part of the stomach, this seems unlikely.

Table 4. *Stomach contents of twelve shags shot in localities with a sandy or muddy sea floor*

Food	No. of specimens	No. of stomachs concerned
Annelida:		
Nephthys hombergi Lamarch.	4	(1)
Crustacea:		
Crangon vulgaris L.	17	(3)
Fish:		
Clupea sprattus L.	41	(1)
Spinachia vulgaris (L.)	2	(1)
Ammodytes sp.indet.	188	(8)
Gadus pollachius L.	6	(2)
Gadus virens L.	1	(1)
Gadus sp.indet.	1	(1)
Gobius ruthensparri Euphrasen	1	(1)
Otoliths:		
Ammodytes sp.	798	(2)
Gadus pollachius L. and *virens* L.	75	(7)
Cottus sp.	1	(1)
Unidentifiable	693	(6)
Totals:		
Annelida	4	(1)
Crustacea	17	(3)
Fish	240	(12)
Otoliths	1567	(12)

Feathers were present in seven stomachs, straw and bracken in one and *Zostera* in one.

The following list gives the total numbers of otoliths recorded. Identification in the case of Gobiidae and Pleuronectidae must be accepted with reserve. The various groups are arranged in descending order of prevalence, with the exception of the large group of worn unidentifiable otoliths, which are also omitted from the percentage column:

Group	Number	Percentage
Ammodytidae	3479	78·2
Gadidae	598	13·5
? Gobiidae or Pleuronectidae	155	3·5
Cottidae	73	1·6
Labridae	59	·1·3
Callionymidae	43	1·0
Clupeidae	27	·0·6
Syngnathidae	13	0·3
Total	4447	
Unidentifiable	1688	
Grand Total	6135	

It will be seen that while this list gives some indication of the past diet, it differs somewhat from the list of actual fishes found in the stomachs (Fig. 1, a). Many of the discrepancies are obviously due to the nature of the otoliths and of the fish themselves. Thus the fragile Clupeoid fishes rapidly disappear from the gut, but their otoliths persist in large numbers, while blennies—abundant in the diet of Clyde shags—are not represented in the list of otoliths. The reason for the absence of blenny otoliths is not understood.

6. DISCUSSION OF STOMACH CONTENTS

As has been mentioned above, locality seems to be by far the most important factor in determining the constituents of the diet. This is made clear by a comparison of histograms c, d and e (Fig. 1) and of the third, fourth and fifth columns of Table 5. In localities with a rocky sea floor blennies, gobies, sticklebacks and Gadoids formed just over 73 % of the total food items, while in areas with a 'mixed' sea floor they formed only about 10 % and in localities with a muddy or sandy sea floor they represented only a little over 4 % of the diet. On the other hand, sand-eels were not found in birds which had fished over a rocky sea floor, but in the case of 'mixed' and sandy localities they made up about 58 and 72 % of the diet respectively. Lack (1945) has drawn attention to the fact that Steven's (1933) results show that the cormorant feeds primarily on fish which live on, or close to, the bottom, while the shag feeds mainly on free-swimming forms. As far as the shag is concerned this is confirmed by the present work, *Ammodytes*, clupeids, gadids and labrids together composing over 70 % of all individuals present. *Ammodytes* and clupeids were the most important although their positions relative to

one another were reversed as compared with Steven's data; in our work *Ammodytes* and clupeids composed 54 and 11 %, respectively, of all the individuals present whereas in Steven's results the corresponding figures are 33 and 49 %. It may be concluded that the shag feeds mainly on these shoal fish in mid-water. In this connexion it is interesting to note that Dewar (1924) states as a general rule for diving birds, including the shag, that the period of the dive is closely related to the depth of the water in the case of birds feeding on the bottom. Deviations from the rule he ascribes to 'pelagic diving' in which the bird does not reach the bottom. The lack of correlation between dive periods and depth of water in the present series is, therefore, indicative that the birds under observation were not engaged in bottom-fishing. The high proportion of

Table 5. *The percentage composition of the diet. In the case of the 'All shags' column, the various groups of food organisms are arranged in descending order of prevalence*

Food	All shags	Shags from sea roost	Shags from rocky sea floor	Shags from mixed sea floor	Shags from sandy sea floor
Ammodytidae	54·1	56·3	—	57·8	72·0
Clupeidae	11·4	10·3	7·8	9·8	15·7
Blenniidae	8·3	9·4	23·5	6·9	—
Crustacea	7·2	5·4	8·7	16·7	6·5
Gadidae	4·1	3·2	11·3	2·9	3·1
Callionymidae	3·4	5·4	0·9	4·9	—
Gobiidae	2·7	0·4	20·0	—	0·4
Labridae	2·7	3·8	6·1	—	—
Gasterosteidae	2·2	0·2	16·5	—	0·8
Cottidae	1·8	2·4	5·2	—	—
Syngnathidae	1·1	2·2	—	—	—
Annelida	0·6	0·2	—	1·0	1·5
Agonidae	0·3	0·6	—	—	—
Mollusca	0·1	0·2	—	—	—

typically rock- or weed-frequenting forms found in shags from a rocky sea floor we had considered as indicating that, sometimes at least, the birds may feed very close to the bottom. Lack, however (in a private communication), has pointed out that these may have been taken when moving outside their normal environment which would account for the presence of many procryptic forms. The abundance of Crustacea was rather surprising—they formed 7 % of the total food items. They were particularly important in the case of Group 3 shags (from 'mixed' sea floor), forming almost 17 % of the total food organisms. Annelids were scarce and even in the case of Group 4 shags (from sandy or muddy sea floor) they made up less than 2 % of the diet.

With regard to the possible economic importance of fish eaten by the shag, our results are in close

Ammodytidae
Clupeidae
Blenniidae
Crustacea
Gadidae
Callionymidae
Gobiidae
Labridae
Gasterosteidae
Cottidae
Syngnathidae
Annelida
Agonidae
Mollusca

(c)

Ammodytidae
Clupeidae
Blenniidae
Crustacea
Gadidae
Callionymidae
Gobiidae
Labridae
Gasterosteidae
Cottidae
Syngnathidae
Annelida
Agonidae
Mollusca

(a)

Ammodytidae
Clupeidae
Blenniidae
Crustacea
Gadidae
Callionymidae
Gobiidae
Labridae
Gasterosteidae
Cottidae
Syngnathidae
Annelida
Agonidae
Mollusca

(d)

Ammodytidae
Clupeidae
Blenniidae
Crustacea
Gadidae
Callionymidae
Gobiidae
Labridae
Gasterosteidae
Cottidae
Syngnathidae
Annelida
Agonidae
Mollusca

(b)

Ammodytidae
Clupeidae
Blenniidae
Crustacea
Gadidae
Callionymidae
Gobiidae
Labridae
Gasterosteidae
Cottidae
Syngnathidae
Annelida
Agonidae
Mollusca

(e)

Fig. 1. Histograms showing percentages of various food organisms in the diet of the shag, compiled from data given in Table 5. (a) All shags examined. (b) Shags from the roost, Little Cumbrae. (c) Shags which had fished over a rocky sea floor. (d) Shags which had fished over a sea floor of mixed character. (e) Shags which had fished over a sandy or muddy sea floor.

agreement with those of Steven (1933). Though the records for all shags (Table 5, col. 1 and Fig. 1, *a*) show that almost 92 % of the total shag diet was composed of fish, the most cursory examination shows that most of the groups concerned are not of the slightest economic importance. Only the Clupeoids and Gadoids are of potential interest and, taken together, these families form about 16 % of the diet.

In the case of the Clupeoids the Tables 1–4 show that herrings, in spite of their abundance in the Firth of Clyde, were definitely identified from only one stomach and, as Steven rightly points out, the attacks of shags and cormorants can be of little importance when the enormous numbers of fish in a herring or sprat shoal are taken into account. The evidence of the otolith counts further supports the view that fishes of this family do not form an important constituent of the shag diet.

With regard to the Gadoids, while it is obvious that these form a steady article of diet, it should be noted that they make up only 4 % of the total of food items. Further, the great majority of Gadoids taken from the stomachs were *Gadus pollachius* and *G. virens* which are of no market value, though they are quite extensively eaten in most coastal districts. The counts showed that 598 (about 14 %) of the recognizable otoliths were Gadoid, but 584 of these belonged to the two species mentioned above and of the fourteen remaining thirteen were identified as *G. minutus*, another unimportant species. It must further be remembered that Gadoid otoliths are rather stoutly formed and thus may be able to persist in the stomach in a recognizable condition for longer periods than those of other families.

Little can be said about flatfish as no specimens were found in the series of 81 stomachs. Certain of the otoliths may have been Pleuronectid, but this is not quite certain. Shags do attack young flatfish in shallow water from time to time, as has been shown by our own field observations (*vide supra*) and by the work of Steven who, however, points out that these fish form only an insignificant percentage of the diet. In the case of the cormorant it is known that flatfish form a very important food item (almost 40 % in Steven's series) but it seems likely that the damage caused by the shag is quite trivial. Steven describes an instructive case where a shag and a cormorant which had fished together were examined. The cormorant contained twenty-six gobies and fifteen small flatfish, the shag thirty-five gobies and no flatfish.

Of the 900 fishes taken from shag stomachs in the present investigation, only 152 (16 %) could be considered as possible food-fish. This is a liberal estimate, as almost all the specimens found were very small. Our general conclusion is that the shag is not a danger to fisheries, however injurious the closely allied cormorant may be, and that such writers as Collinge (1924–7) have vastly overstated the proportion of food-fishes in its diet.

It was most interesting to find that many of the fish recovered from shag stomachs belonged to species with well marked protective adaptations. Among protectively coloured types *Spinachia*, *Cottus*, *Agonus* and *Callionymus* may be mentioned as examples whose obliterative colouring and patterns appear almost perfect to human eyes. Some species adopting a protective habit occurred also, notably *Syngnathus* which is nearly invisible when floating vertically among weed. Powerful defence mechanisms were present in some such as *Cottus*, whose powerful spines must make it a very difficult fish to swallow. It was interesting also to find fish such as *Centronotus* in the diet, as this species spends much of its time under stones, making only short excursions into the dense weed forests in search of small crustaceans.

7. NEW RECORDS

The only certain new record for the Clyde sea area is that of *Leander serratus* (Pennant) of which six specimens were recovered from shag stomachs.

Four partially digested fish found in a shag from Balloch Bay were identified as almost certainly *Callionymus maculatus* Rafinesque. This determination was supported by the presence in the stomach of two ovigerous females of the parasitic copepod *Chondracanthus ornatus* T. Scott. This species, to our knowledge, has been recorded from *C. maculatus* only.

8. PATHOLOGICAL NOTE

One shag, when shot on the roost, was in a moribund condition. It was very light and the alimentary canal was completely empty. The liver and spleen were found to be thickly infiltrated with small white nodules like sago grains. On examination, these proved to be miliary granulomata—almost certainly avian tuberculosis. This record is interesting, as tuberculosis is usually confined to domestic birds. As all the material had been fixed it was not possible to confirm the diagnosis by culture. We are indebted to Dr J. F. Heggie for pathological notes concerning this bird.

9. ACKNOWLEDGEMENTS

10. SUMMARY

1. The stomach contents of eighty-one shags (of which seventy-eight were obtained in the Firth of Clyde) were examined.

2. The diet consisted very largely of fish. 900 fish, belonging to at least twenty species, were recovered. Crustacea were of quite common occurrence in the stomachs of shags from certain areas. Large annelids were also found from time to time but were never common. Remains of a squid were recovered from one stomach.

3. Large numbers of fish otoliths occurred in the stomachs. These were counted and, whenever possible, identified.

4. The feeding habits of the shag were studied in nature.

5. The general conclusion is that the shag feeds mainly on fish of no commercial value and that the damage it does to food-fishes is quite negligible.

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OBSERVATIONS ON THE FOOD OF EELS (*ANGUILLA ANGUILLA*) FROM THE WINDERMERE CATCHMENT AREA

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1. INTRODUCTION

Some investigation of the food of the eel (*Anguilla anguilla* (L.)) in fresh water has been carried out on the Continent, but no such study, apart from that based on 27 eels from East Anglia (Hartley, 1940) appears to have been made for British waters. The following account, although based on limited observations, provides some information on the subject. The eels examined were collected, over a number of years, from the Windermere catchment area. They formed part of the material obtained for a study primarily of age and growth (Frost, 1945 *a*, *b*), thus the collection of data on food was subordinate and the information obtained from them will not give a comprehensive picture of the food of eels in this district. The eels came from three places in the catchment region, namely, Windermere, the Cunsey Beck which flows out of Esthwaite Water into Windermere, and the River Leven, the outflow of Windermere (see Frost, 1945 *a*, Fig. 1). Yellow eels were examined from all three stations, including small individuals that is those under 35 cm. (but not including elvers) locally called 'snigs', and in addition an examination was made of migrating (silver) eels that came from the Cunsey Beck.

2. MATERIAL AND METHODS

The material obtained at each of the three stations and the method of collecting it will be described under the appropriate heading when the results from each station are given. The food organisms in the stomach, which in the eel consists of a blind sac and a relatively much smaller pylorus, were little digested and thus were recognizable and could be counted; in some cases this was also true of the contents of the intestine, but in others it was not so. In view of this the results are based on the contents of the stomach and not of the alimentary canal. The food organisms were counted individually (except in the case of silver eels, Table 5) and the number of fish containing any organism was noted. In the table the number of individual organisms of any one type is given and expressed as a percentage of the total number of organisms eaten; the number of fish containing each type of food organism is shown, this number also being expressed as a percentage of the total number of fish examined.

The food organisms have been determined to the species or to groups. I wish to acknowledge the help of Mr J. R. Le Brockton Tomlin in connexion with the identification of the Mollusca and of Dr N. E. Hickin for his examination of the Polycentropid larva from Cunsey Beck which he finds to resemble that of *Polycentropus flavomaculatus* Pict. The following notes are given on the organisms recorded from the stomachs.

Fish. The fish were the minnow (*Phoxinus phoxinus* (L.)), the perch (*Perca fluviatilis* L.) and one specimen which was probably a small brown trout (*Salmo trutta* L.).

Mollusca. In the Windermere eels *Limnaea pereger* (Müll.), *Valvata piscinalis* (Müll.), *Ancylastrum fluviatile* (Müll.), *Sphaerium corneum* (L.), *Pisidium* sp. and *Planorbis* sp. were found. *Limnaea*, *Planorbis*, *Pisidium* and *Sphaerium* were found in the silver eels taken at Cunsey Beck, and *Limnaea* was the mollusc identified from the yellow eels taken at this station. It was not always possible to distinguish *Pisidium* and *Sphaerium* from each other and therefore they have been considered together.

Trichoptera. These were all, save one adult and two pupae, larval forms. In the lake eels a Leptocerid most probably *Leptocerus* sp., a Polycentropid and *Phryganea* sp. were identified and in the beck and river eels *Rhyacophila* sp., *Hydropsyche* sp., *Hydroptila* sp. and a Polycentropid. The latter, which occurred in large numbers in the yellow eels of the Cunsey Beck was, as noted above, most probably *Polycentropus flavomaculatus* Pict.

Ephemeroptera. All but one specimen were nymphal forms. In the Windermere eels *Ephemera danica* Müll., *Leptophlebia* sp. and an Ecdyonurid, were taken and from those of the Cunsey and Leven *Baëtis* sp. and *Ephemerella ignita* (Poda). The one adult Ephemeropteran was a subimago, too much digested for identification, eaten by a silver eel.

Plecoptera nymphs, which occurred only in the River Leven fish, were *Amphinemura cinerea* (Oliv.).

Diptera larvae, which were present in fish from all stations, were almost all Chironomidae, these were not identified further than the group. Tipulid larvae occurred in the Cunsey and Leven eels and *Simulium* larvae in the Cunsey fish. Pupal Diptera were represented by the Chironomidae.

Other aquatic insect larvae found in the stomachs

were *Sialis* sp. and unidentified Odonata and Coleoptera, the first being taken in eels from Windermere and Cunsey Beck, the second from all three stations and the last from the Leven fish.

Aquatic Hemiptera were represented by one fragmentary specimen of *Sigara* sp. found in a Leven fish.

Winged insects were represented by one Trichopteran, one Ephemeropteran and two insects of terrestrial origin and all were found in eels caught in the Cunsey Beck.

Crustacea. Gammarus pulex De Geer was recorded from Windermere and Cunsey fish and *Asellus* sp. from the lake and Leven eels.

depth of 75 ft. (24 m.); there is a narrow littoral zone. The water of the lake has a low nutrient salt content and is 'soft' in character. The 106 yellow eels upon which the following account is based were taken from various parts of the lake and from deep and shallow water. The fish were captured by seine (41), Dutch Fyke net (22)†, perch trap (20), long line (17) and rod and line (6), over a period of several years. Many other eels were examined but those caught in perch traps which had obviously been feeding on captive perch and those specimens taken on long lines which had clearly fed upon the bait could not be considered. The eels examined were captured in May (14), June (22), July (8), August

Table 1. *Food of yellow eels in Windermere; 106 fish*

Food organism	No. of individual organisms	% of total organisms	No. of fish containing	% of fish containing
Limnaea pereger	361	18·0	21	19·8
Valvata piscinalis	604	30·1	31	29·3
Pisidium/Sphaerium	445	22·2	36	34·0
Planorbis spp.	20	1·0	9	8·5
Ancylastrum fluviatile	2	0·1	1	0·9
Mollusca indet.	72	3·6	22	20·7
Leptocerid larvae	191	9·5	18	17·0
Polycentropid larvae	4	0·2	2	1·9
Phryganea sp. larvae	5	0·2	3	2·8
Trichopt. l. indet.*	28	1·4	16	15·1
Sialis larvae	38	1·9	13	12·2
Ephemera danica nymphs	22	1·1	9	8·5
Leptophlebia sp. nymphs	8	0·4	2	1·9
Ecdyonurid nymphs	2	0·1	2	1·9
Odonata nymphs	3	0·1	2	1·9
Chironomid larvae	40	1·9	8	7·5
Gammarus pulex	147	7·3	21	19·8
Asellus	4	0·2	1	0·9
Oligochaeta	12	0·6	3	2·9
Perca	1	0·05	1	0·9
Others	2	0·1	2	1·9
Totals	2011	100·05		

* Contained two Trichoptera pupae.

Oligochaeta were found in eels from all stations and although the size of their setae suggested earthworms the shape of these did not preclude the worms being Enchytraeids or Lumbriculids.

'*Others*' included creatures which had become accessible food by chance such as caterpillars, slugs, a woodlouse and a spider, and any unidentifiable debris.

3. RESULTS

The data obtained from the investigation of the stomach contents are considered under the following headings: (a) food of yellow eels in Windermere, (b) in the Cunsey Beck, (c) in the River Leven, and (d) food of migrating eels.

(a) Food of yellow eels in Windermere

Windermere has a length of 10·5 miles (17 km.), a mean breadth of 950 yd. (874 m.) and a mean

(48), September (4), October (8) and December (2). They ranged in length from 35·5 to 60 cm., the mean being 45 cm. and the majority of the fish were between 40 and 50 cm. long. The age of these eels deduced from a previous study (Frost, 1945b) is probably of the following order: 33·5 cm. = 6, 60 cm. = 11, 45 cm. = 9, 40 cm. = 8 and 50 cm. = 10 years in fresh water.

In Table 1 the results of the stomach analyses irrespective of the size of the fish or the month of its capture are given. It will be seen that molluscs, as indicated by the number consumed and the number of fish containing them, form much the greatest part of the diet, and of these *Valvata piscinalis* is the predominating species with *Limnaea* and *Pisidium/Sphaerium* next in importance. The

† A war-time fishery for perch in Windermere by means of unbaited wire traps lasts from mid-April to June and eels frequently enter these traps.

occurrence of 80 specimens of *Limnaea* in one fish and of 70 *Valvata* in another gives some idea of the quantities of these molluscs eaten. Of the remaining food organisms Trichoptera larvae and *Gammarus pulex* occur in a fair proportion of the fish, the former making up by number 11·5 % of the organisms eaten, a figure which is, however, affected by the fact that two fish contained 80 and 40 specimens, whereas the

87 cm., had been feeding on the trapped perch. The length of most of the individuals eaten was 10·0 cm., whereas the mean length of the captives is 13·5 cm. The consumption of the confined perch, which were also apparently selected for size, suggests that under natural conditions fish are not easily caught nor are those of suitable size encountered in the lake.

Table 1 gives the data obtained from the stomach

Table 2. *Food of yellow eels in Windermere in relation to size of the fish; number of fish given in brackets*

(a) Mean length of eels containing different foods

Food ...	Mollusca (91)	Aquatic insect larvae (52)	Chironomid larvae (8)	Crustacea (22)	Oligochaeta (3)	Fish (1)	Others (2)
Mean length in cm.	45·5	43·7	39·3	43·5	46·0	50·0	44·5

(b) Percentage composition of diet of three length groups

Length groups in cm.

Food organisms	Less than 35 (6)		36–50 (79)		Over 50 (21)	
	% of total organisms	% of fish containing	% of total organisms	% of fish containing	% of total organisms	% of fish containing
Mollusca	84·1[1]	67·0	73·9	85·0	76·0	91·0
Aquatic insect larvae	9·1	50·0	17·5[2]	50·5	7·6	43·0
Chironomid larvae	1·1	16·7	2·6	8·7	—	—
Crustacea	5·7	33·4	5·4	21·5	15·2[3]	14·3
Oligochaeta	—	—	0·4	2·5	1·2	4·3
Fish	—	—	0·06	1·3	—	—
Others	—	—	0·1	2·5	—	—
Totals	99·9		99·96		100·0	

[1] 40, [2] 60, and [3] 80 specimens in one fish.

Table 3. *Seasonal food of yellow eels in Windermere; number of fish given in brackets*

Food organisms	May (14)		June (22)		July (8)		August (48)		Sept.–Dec. (14)	
	% of total organisms	% of fish containing	% of total organisms	% of fish containing	% of total organisms	% of fish containing	% of total organisms	% of fish containing	% of total organisms	% of fish containing
Mollusca	43·0	78·5	55·8	82·0	59·0	75·0	88·7	96·0	87·3	64·0
Aquatic insect larvae	20·5	64·0*	40·3	68·0	28·0	50·0	4·5	46·0	1·3	14·3
Chironomid larvae	0·9	7·0	0·2	0·4	0·9	12·5	3·3	10·1	—	—
Crustacea	35·6†	28·5	3·7	27·3	9·6	37·5	3·5	14·8	4·7	14·3
Oligochaeta	—	—	—	—	1·7	12·5	—	—	6·7	14·3
Fish	—	—	—	—	—	—	0·09	2·1	—	—
Others	—	—	—	—	0·8	12·5	—	—	—	—
Totals	100·0		100·0		100·0		100·09		100·0	

* 80 and 40 Trichoptera larvae in two fish.   † 60 *Gammarus* in one fish.

remaining 31 fish each contained less than 10. The predominant species of larval Caddis was a Leptocerid. The number of *Gammarus* is usually less than 12 per fish except in two cases when 30 and 60 were present. *Sialis* and Ephemeroptera occurred in several fish but they cannot be regarded as of importance. Chironomid larvae are negligible.

The virtual absence of fish in the diet is interesting since of 90 eels (excluding 20 noted above) examined from perch traps, 34, ranging in length from 42 to

analyses without any distinction as to the size or time of capture of the fish, Tables 2 and 3 present them with these factors taken into consideration. Table 2 shows (a) the mean lengths of the eels containing the different food organisms, and (b) the diet of three size groups of eels, namely those of 35 cm. and less in length (snigs), those 36–50 cm. representing eels of typical lake size and those of more than 50 cm. regarded as larger lake eels. It appears from Table 2(a), when the difference in the numbers of speci-

mens in each group is taken into consideration, that size has no significant influence upon diet, although possibly the mean length of the eels eating Chironomid larvae indicates that they are primarily the food of the smaller fish. The impression that size has little effect on diet is also given by Table 2(*b*) which shows that Mollusca are the main food of eels of all sizes, although the lower frequency figures for the smallest fish are suggestive. There is some indication that aquatic insect larvae are not so important to eels of over 50 cm. and none of these fish had eaten Chironomid larvae. Table 3 gives the seasonal food of the Windermere eels as presented by monthly data, except for those of September to

stream about 8 yd. wide, which flows out of Esthwaite Water and into Windermere. In order to obtain information about the food of eels in running water several attempts were made to capture the fish from the beck. The method used, a hand net, since a tank and trough trap was not feasible, was tedious and yielded only 11 eels. There is, however, a trap for the capture of migrating (silver) eels situated some 90 yd. below the outflow of the beck from Esthwaite Water and in August and September 1943, 31 yellow eels, mostly small, containing food were found in this trap. It appears likely that they were swept into the trap either from the beck or the lake, by floods. Five of these trapped fish contained

Table 4. *Food of yellow eels in Cunsey Beck; 42 fish*

	Stream feeding (16)				Probably stream feeding (9)				Lake or stream feeding (17)			
	Individual organisms		Fish containing		Individual organisms		Fish containing		Individual organisms		Fish containing	
Food organism	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Polycentropid larvae	69	47·5	11	68·0	43	79·5	9	100	—		—	
Hydroptila sp. larvae	—	—	—	—	—	—	—	—	3	3·5	1	5·9
Hydropsyche sp. larvae	1	0·7	1	6·2	—	—	—	—	—	—	—	—
Trichopt. l. indet.	2	1·7	2	12·5	1	1·9	1	11·1	2	2·3	2	11·8
Ephemerella ignita nymphs	44	30·5	8	50·0	—	—	—	—	—	—	—	—
Baëtis spp. nymphs	10	6·8	1	6·2	—	—	—	—	—	—	—	—
Ephemeropt. n. indet.	—	—	—	—	1	1·9	1	11·1	2	2·3	2	11·8
Chironomid larvae	—	—	—	—	2	3·7	1	11·1	43	50·0	4	23·5
Chironomid pupae	—	—	—	—	1	1·9	1	11·1	—	—	—	—
Simulium larvae	6	4·1	2	12·5	—	—	—	—	—	—	—	—
Tipulid larvae	1	0·7	1	6·2	—	—	—	—	1	1·2	1	5·9
Oligochaeta	1	0·7	1	6·2	1	1·9	1	11·1	27	31·5	6	35·5
Gammarus pulex	3	2·1	2	12·5	2	3·7	1	11·1	1	1·2	1	5·9
Sialis larvae	—	—	—	—	1	1·9	1	11·1	1	1·2	1	5·9
Limnaea pereger	—	—	—	—	—	—	—	—	1	1·2	1	5·9
Mollusca indet.	3	2·1	2	12·5	1	1·9	1	11·1	2	2·3	2	11·8
Fish	3	2·1	2	12·5	—	—	—	—	—	—	—	—
Odonata nymphs	1	0·7	1	6·2	—	—	—	—	—	—	—	—
Winged Trichoptera	1	0·7	1	6·2	—	—	—	—	—	—	—	—
Others	—	—	—	—	1	1·9	1	11·1	3	3·5	2	11·8
Totals	145	100·0			54	100·0			86	100·2		

December which have been considered together. The mean lengths of the eels for the different months is of much the same order so that size has not affected the seasonal results. Seasonal differences in the diet are not much marked. Molluscs are eaten at all times and always in numbers relatively large to those of other foods. There is a tendency for a higher proportion of the fish to be feeding on aquatic insect larvae during May and June than in the remaining time which is primarily due to the number feeding on nymphal Ephemeroptera, chiefly *Ephemera danica* in May, their emergence time, and on these nymphs and Trichoptera larvae in June.

(b) Food of yellow eels in Cunsey Beck

The Cunsey Beck, from which the 42 eels considered in the following account were taken, is a

Ephemerella ignita or *Simulium* or both and are therefore considered, with the 11 hand-caught specimens, as beck fish; nine of them, since they contained *Polycentropus flavomaculatus*, are regarded as probably feeding in the stream and the remaining 17, the origin of which could not be recognized, are presented as lake or stream feeders (Table 4). The 42 eels examined were taken in June (1), July (8), August (26), September (6) and October (1). They ranged in length from 13 to 62 cm. with a mean length of 28·8 cm., the majority being 26–29 cm., four specimens only being over 40 cm.; the average length for the 16 undoubted beck specimens is 24·8 cm. It may be presumed that the age for length relationship of these 26–29 cm. = 5 years in fresh water. The eels were too few in number to consider diet in relation to size or season.

In the 16 beck fish Trichopteran larvae formed the greatest percentage by number of the food organisms eaten and occurred with greater frequency than any other food, the dominant species being a Polycentropid, probably *Polycentropus flavomaculatus*. This result is corroborated by the nine trapped fish probably of beck origin. The rest of the diet was composed mainly of aquatic insect larvae, predominantly Ephemeroptera and Diptera. In the seventeen eels which may have been of stream or lake origin Oligochaeta and Chironomidae predominated. The former were not identified but from their setae and general appearance most of them seemed to be earthworms, a point substantiated by their high incidence in the trapped eels which suggests that they became available food as a result of the floods.

The results of the stomach examinations are given in Table 5. Chironomid larvae and Ephemeroptera nymphs may be regarded as the most important foods, the former primarily from the numbers consumed and the latter from the high proportion of fish in which they occurred. The remaining food organisms, which are chiefly aquatic insect larvae, are not present in any great numbers nor have many fish fed on them. One eel only, a specimen 23 cm. long, had eaten a fish, a minnow.

An interesting point arises if these results are considered conjointly with those obtained from the yellow eels of Cunsey Beck. At both places aquatic insect larvae are the main food, but whereas Ephemeroptera nymphs (small specimens usually) are eaten to the same extent at both stations the im-

Table 5. *Food of yellow eels in River Leven; 32 fish*

Food organisms	No. of individual organisms	% of total organisms	No. of fish containing	% of fish containing
Chironomid larvae	118	61·5	9	27·0
Chironomid pupae	3	1·6	2	6·2
Ephemerella ignita nymphs	29	15·1	8	25·0
Baëtis sp. nymphs	9	4·6	6	18·7
Ephemeropt. n. indet.	5	2·6	5	15·6
Plecoptera nymphs	10	5·2	5	15·6
Rhyacophila sp. larvae	1	0·5	1	3·1
Hydropsyche sp. larvae	2	1·1	2	6·2
Trichopt. l. indet.	3	1·6	1	3·1
Asellus sp.	8	4·1	3	9·5
Corixid	1	0·5	1	3·1
Oligochaeta	2	1·1	2	6·2
Fish	1	0·5	1	3·1
Others	1	0·5	1	3·1
Totals	193	100·0		

(c) Food of yellow eels in the River Leven

The Leven, a fairly quickly flowing river of some 30–40 yd. wide is the outflow from Windermere. The 32 eels considered below were caught in its upper, non-tidal part. During the course of investigations carried out on elvers of the River Leven some specimens of small yellow eels, 'snigs', were captured in the tank and trough traps set for elvers, in addition to these a few others were taken by hand: 23 of the trapped 'snigs' and nine of the hand-caught ones contained food and although these fish provide only a little information it has been thought worth while to record it. The eels were taken in May (9), June (4), July (9), August (5) and September (5). They ranged from 8·0 cm. (one specimen) to 25 cm. in length, with a mean of 14·4 cm. The age for length relationship for such eels may be given as 8·0 cm. = 1, 25 cm. = 5 and 14·4 cm. = 2 years in fresh water. Since the fish were so few in number, the data from the specimens have been considered irrespective of time of capture or of their size.

portance of Chironomid larvae and larval Trichoptera is reversed at the two stations. This reversal may be an expression of faunistic differences in the two waters; but it seems more likely that it is related to the marked difference in the size of the eels examined from the Leven and the Cunsey, the specimens from the former being much smaller (14·4 cm. average) than those from the beck.

(d) Food of migrating eels

This account is based on 60 eels caught over a period of years in the traps set on the Cunsey Beck. The trap which is situated some 90 yd. below the outflow of the stream from Esthwaite Water was erected and is operated by the Freshwater Biological Association and it fishes the whole width of the stream. It is in operation from July to November and is for the capture of eels which are migrating to the sea, such fish being characteristically in the silver phase having a silver belly and large eyes. Some of the eels caught, although clearly

seaward migrants, had not developed fully these characteristic features but were turning from the yellow to the silver phase. When the trap was first used no distinction between the fully silver and the transitional form was made, although later the two forms were distinguished, with the result that of the 60 migrants containing food 21 (18 ♀ and 3 ♂) may be taken as silver eels, the remainder being the transitional forms, although probably including some silver specimens. Thus, although the following account is better regarded as referring to the feeding habits of seaward migratory eels, it does provide some evidence that the silver eel takes food, a fact of some interest since it is usually alleged that it does not do so. Petersen (1894), for example, attributes the fact that baited hooks catch far more yellow than silver eels to the greater voracity of the former, 'a fact which is fully borne out when we examine the contents of the stomachs of eels which have been caught in other ways; the silver eels generally contain nothing, though it may happen [that they do contain food?], particularly when the eel has perhaps not quite finished the change of its dress. When it is migrating and in its full, characteristic dress, I never saw any food in its stomach'. Of course, many undoubted silver eels taken in the Cunsey trap did not contain food and the alimentary canal had the shrunken appearance associated with silvering.

The 60 migrating fish taken during the period of the 'run' August to October consisted of 57 females ranging from 50 to 70 cm. in length with a mean of 58·2 cm. and 3 males, 40 and 41 cm. long. The age of the former would lie between 11 and 14, an eel of 58·2 cm. being 11 years in fresh water, and the three males would have spent about nine years in fresh water.

The results of the stomach examinations are given in Table 6. From the situation of the trap 90 yd. below the outflow from Esthwaite Water it is most likely that the stomach contents represent the feeding in the lake rather than in the beck, since having been stimulated to leave the lake it is improbable that the eels would pause in the short stretch of stream above the trap. The table shows only the number of eels containing any particular food organism and the expression of these data in percentage terms, since other data were not always recorded. The diet is varied and contains most of the kinds of food organisms which were found in the yellow eels of Windermere, the River Leven or the Cunsey Beck. Molluscs, Trichoptera and Diptera occurred with the greatest frequency and among these the occurrence of *Chaoborus* ?*crystallinus* De Geer was of interest since none of the yellow eels of Windermere contained larval Diptera of this genus. Fish had been eaten to an appreciable extent, in one case four minnows were found in one stomach, but before concluding that migrating eels eat more fish than yellow eels it must be noted that the minnows, perch,

etc., which are sometimes washed into the trap, may have been eaten when captive.

4. DISCUSSION

In Table 7 the results obtained are summarized, the food organisms having been grouped into six main categories. The number of individual organisms in each category is given, this figure being expressed as a percentage of the total organisms, and the number of fish containing each category is noted, each such number being expressed as a percentage of the total number of fish examined. It is evident from the table that the eel feeds chiefly on bottom-living

Table 6. *Food of migrating eels taken in the trap on Cunsey Beck; 60 fish*

Food organisms	No. of fish containing	% of fish containing
Limnaea pereger	4	6·6
Valvata piscinalis	2	3·3
Pisidium/Sphaerium	6	10·0
Planorbis spp.	2	3·3
Mollusca indet.	7	11·7
Leptocerid larvae	3	5·0
Polycentropid larvae	2	3·3
Phryganea sp. larvae	1	1·7
Trichopt. l. indet.	11	18·4
Chironomid larvae	8	13·4
Chironomid pupae	2	3·3
Tipulid larvae	3	5·0
Chaoborus larvae	4	6·6
Phoxinus	4	6·6
Perca	2	3·3
Salmo trutta	1	1·7
Fish indet.	5	8·3
Baetid nymph	2	3·3
Ephemeropt. n. indet.	2	3·3
Coleoptera larvae	4	6·6
Sialis larvae	3	5·0
Odonata nymphs	1	1·7
Corixid	2	3·3
Oligochaeta	2	3·3
Gammarus pulex	1	1·7
Ostracods	1	1·7
Winged insects (terrest.)	2	3·3
Winged Ephemeroptera	1	1·7
Others	7	11·7
Debris	2	3·3

invertebrates and of these molluscs predominate in the eels from Windermere and aquatic insect larvae in those from Cunsey Beck and the River Leven. This distinction is, however, in all probability due to the difference in the size of fish examined from the lake and the running waters (it has already been suggested that such a difference explains the different diet of Cunsey and Leven eels) and also almost certainly an expression of a difference in the faunistic conditions prevailing between Windermere and the two streams. In connexion with the latter it may be

Table 7. *Summary of food of yellow and migrating eels in Windermere catchment area; number of fish examined in brackets*

Food organisms	Windermere (106)				Stream (16)				Cunsey Beck (42)								River Leven (32)				River Leven Migrating eels (60)	
	Individual organisms		Fish containing		Individual organisms		Fish containing		Probably stream (9)				Lake or stream (17)				Individual organisms		Fish containing		Fish containing	
									Individual organisms		Fish containing		Individual organisms		Fish containing							
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Mollusca	1504	74·80	91	86·0	3	2·1	2	12·5	1	1·9	1	11·1	3	3·5	3	17·6	—	—	—	—	18	30·0
Aquatic insect larvae	341	17·00	52	49·0	134	92·4	16	100·0	49	90·6	9	100·0	52	60·4	9	53·0	180	93·4	30	94·0	32	53·5
Crustacea	151	7·45	22	20·8	3	2·0	2	12·5	2	3·7	1	11·1	1	1·2	1	5·9	8	4·1	3	9·5	2	3·3
Oligochaeta	12	0·60	3	2·9	1	0·7	1	6·2	1	1·9	1	11·1	27	31·4	6	35·5	2	1·0	2	6·2	2	3·3
Fish	1	0·05	1	0·9	3	2·1	2	12·5	—	—	—	—	—	—	—	—	1	0·5	1	3·1	12	20·0
Others	2	0·10	2	1·9	1	0·7	1	6·2	1	1·9	1	11·1	3	3·5	2	11·8	2	1·0	2	6·2	9	15·0
Totals	2011	100·0			145	100·0			54	100·0			86	100·0			193	100·0				

Locality ...

noted that from the quantitative data given by Moon (1934) and Humphries (1936) one may deduce that in Windermere molluscs are relatively much more abundant than aquatic insect larvae (exclusive of the Chironomidae) and that from general observation I have gained the impression that the molluscan fauna of the Cunsey and the Leven is appreciably poorer than that of the lake. It appears that the food of eels, like that of other fish, is governed, to some extent at least, by the food organisms present.

Surface food, as represented by terrestrial insects which have fallen on to the water or by the adult forms of insects with aquatic larvae, is almost absent from the stomachs. This doubtless is related to the fact that the eel lives primarily on the bottom of the lake or stream. The incidence of surface food was negligible among the many thousands of New Zealand eels examined by Cairns (1941, 1942*a,b*).

It was rather unexpected to find that so few fish are eaten, since records from other European waters indicate that they occur to some considerable extent in the diet (see below). This may be due, to some extent, to the size of the eels examined from the Windermere catchment. Cairns (1941, 1942*a,b*) found that in New Zealand the trout eaten by long-finned eels (*Anguilla dieffenbachii* Gray) of 40–75 cm. long were all fingerlings or fry, since apparently eels of this size could not swallow anything larger; whereas in eels of over 75 cm. there was a 'predominance of trout [adult fish] in the diet'. A somewhat crude attempt to see the size of salmonid fish that a yellow eel could swallow was made by opening the mouth of the eel and inserting individuals of different sizes. It was found that an eel of 40 cm. long could just take a fingerling trout (5 cm.), one of 50 cm. easily took a 9·5 cm. salmonid and one of 75 cm. or more could take an 11 cm. salmon parr. The mean length of the eels examined from the River Leven and the Cunsey Beck was 14·4 and 28·8 cm. respectively and thus a salmonid fingerling would be too large a prey for such eels. There seems no reason why they should not swallow alevins or young fry; but since none of the eels was captured in spring, when these fish would be present, there is no evidence on this point. Other species of fish, such as minnows and sticklebacks, would appear to present prey of suitable size to the eels of the Cunsey and the Leven, but probably the number examined was insufficient to establish the incidence of fish in the diet. The eels examined from Windermere covered a wide range in size and had a mean length of 45 cm., and it seems unlikely that such eels would fail to find prey of suitable size among the varied fish population of the lake. The fact that when confined, as in perch traps, or tethered as line bait, perch and minnows are eaten suggests that the eel, being primarily benthic, finds that in the lake these and all except the bottom-living species of fish, such as bullhead and loach, etc., are difficult to capture and out of its range. In

view of this suggestion it may be noted that the bullhead (*Cottus gobio* (L.)), the loach (*Nemachilus barbatula* (L.)), the lamprey (*Lampetra fluviatilis* (L.)), and the gudgeon (*Gobio gobio* (L.)), all benthic fish, comprise by far the greatest part of the fish diet of over 100 eels examined from the River Cam (Hartley, 1940 and unpublished data).

Observations on the food of eels in fresh waters made by various investigators are of interest for comparison with those obtained from Windermere. The many references to the food of individual eels from British waters will not be noted here, but Hartley's detailed examination of 27 (1940) and 87 (unpublished data) eels from East Anglia, mainly from the River Cam, shows that aquatic insect larvae, *Astacus*, *Gammarus* and fish are the foods occurring most frequently in the stomachs. Hornyold (1926), generalizing from observations made in France and Spain, notes that in rivers, lakes and ponds eels feed on snails, slugs, crayfish, aquatic insect larvae, frogs and fish; he also notes that annelids, including leeches, are eaten and sometimes elvers in greater or lesser quantities. Schiemenz (1910) in a general account of the food of eels in German waters states that *Asellus* and *Gammarus* are the food of 'pencil-sized' specimens, larger ones feed on molluscs, insect larvae, aquatic worms and fish, such as burbot (*Lota lota* (L.)) and stickleback (*Gasterosteus*) and in spring the eel eats fish spawn. Wundsch (1916) found that in the Steinhuder lake the eels of an average length of 45 cm., fed on fish, aquatic insect larvae and Cladocera and in Paddenpfuhl those of an average length of 36 cm. ate insect larvae, predominantly *Corethra* (*Chaoborus*), and in Aeppelsee aquatic insect larvae, fish and molluscs were the chief foods of eels. Struck, quoted by Schiemenz (1910), notes that in the Schmollensee eels which 'lived on *Mysis* in one year turned to plankton during a year when this was abundant'. These observations indicate a diet that is, in general, much like that of the eels of the Windermere catchment area, but one in which fish is appreciably more important, a contrast probably due to local faunistic conditions and to the type of water investigated. The consumption of Cladocera (*Leptodora*, *Bosmina*, etc.) by the 45 cm. eels of the Steinhuder See had no parallel in the Windermere region, although such organisms are abundant in the lake.

Eels are alleged to feed on carrion, but Schiemenz (1910) maintains that when found near carrion the eel is not feeding upon it but is in search of the *Gammarus*, snails, etc., which are consuming the dead matter. Fishermen on Windermere consider that the bait set in yellow eel traps is useless when it becomes rotten.

There is an opinion among scientific investigators and practical fishermen that yellow eels show two forms, a broad-headed type having a flat, muscular head and thick lips (*breitkopf*) and a narrow-headed

type with more pointed head and thinner lips (*spitzkopf*). It is maintained that the two forms have different feeding habits, that the broad-heads are predators and feed on fish and the narrow-heads are not so (*friedfisch*) but feed on aquatic insect larvae, snails, etc. Schiemenz, however, states (1910) and demonstrates (1935) that there is no such hard and fast distinction, there being at most a tendency for the *spitzkopf*, since they are the smaller to be the *friedfisch* and the *breitkopf* being larger to be the predators; a similar conclusion was reached by Torlitz (1922) and may be deduced from the data given by Wundsch (1916). Sivertsen (1938) showed that in Norway in fresh water insect larvae and snails formed the main food of both types of eel. The eels examined from the Windermere catchment were not divided into the broad and narrow-headed forms but it is my recollection that the fish from the lake, primarily feeding on molluscs, included both types.

The relationship between the feeding habits of the eel and those of the fish associated with it, particularly trout and young salmon, may be discussed in the light of the information obtained from the Windermere catchment area. The conditions in a lake are well illustrated by reference to Windermere since data on the food of brown trout (*Salmo trutta* L.), char (*Salvelinus a. willughbii* (Günther)), perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.) and minnow (*Phoxinus phoxinus* (L.)) are available. Here the food of the trout consists principally of *Limnaea, Gammarus* and the larvae and pupae of aquatic insects (Allen, 1938); the char feeds chiefly on planktonic Crustacea, Chironomid larvae and pupae and to some extent on *Gammarus* (Frost, unpublished data); fish, *Gammarus* and the insect bottom fauna provide the main foods of perch of 16·5–18·5 cm. long; the adult pike feeds primarily on fish and to a very small extent on aquatic insect larvae (Allen, 1935; Frost, unpublished data) and the food of the minnow consists of Cladocera, Copepoda and algae (Frost, 1943). Comparison of this evidence with that in Table 1 suggests that the food requirements of the eel coincide appreciably with those of the trout and to some extent with those of the perch, they exhibit little in common with those of the char and pike and nothing with those of the minnow. It may also be deduced from the same comparison that the eel is seldom a predator upon the other members of the fish community in Windermere (a view somewhat modified by the evidence of trapped perch) and that it is rarely preyed upon by other fish.

The relationship between the food of the eel and that of other members of the fish community in running water cannot be determined directly on evidence from the Cunsey Beck and River Leven, since there are no data on the food of other fish in these waters. Some indication, however, of the relationship is obtained if the information obtained from the Cunsey and Leven eels is compared with

that obtained from trout, salmon (*Salmo salar* L.) and minnow, the important species of the Cunsey Beck and River Leven, from other waters. Investigations of the food of brown trout from rivers and streams of widely different types show that aquatic insect larvae, particularly the Chironomidae, Ephemeroptera and Trichoptera, are of primary importance as food organisms. The same has been found for the feeding of young salmon, and it has also been shown that in a small river these organisms enter, although to a lesser extent, into the diet of minnows (Frost, 1943). Since such larval insects form the chief food of the yellow eels of the Cunsey Beck and the River Leven the food requirements of the three fish have much in common with that of the eel. There is evidence, provided mainly by the larger migrating specimens, that the eel preys upon fish. Studies of the stomachs of fish from other rivers indicate that the eel in running waters is not a forage fish.

The interrelationship between the eel and trout and young salmon as illustrated by the data from the Windermere catchment area may be further considered under the headings: (1) the extent to which the two types of fish exploit the same food supply, (2) the eel as a predator upon the salmonids, and (3) the eel as a food for salmonids:

(1) It has been shown that in Windermere the food of yellow eels and trout is to an appreciable extent the same and that the diet of the eel in Cunsey Beck and the River Leven is much like that of the trout and young salmon of any stream. Whether or not this exploitation of the same source of food results in competition will depend on the adequacy of the food supply and the density of the fish population, points on which there are no adequate data for this locality. The eel population, however, may be assumed to be considerable for there is a 'good run' of elvers up the River Leven, and on the River Wyre, a smaller Lancashire river, a similar 'good run' has been estimated, from trapping experiments, to be some 1,000,000 elvers annually.

(2) The eels from the Windermere catchment do not support the view that they are predators upon trout and young salmon, but this is more than likely explained by the pelagic habits and size of trout in the lake and the limited nature of the data obtained from the beck and river (pp. 46–7). Information from river keepers and from the literature indicates that the eel does prey on salmonids in rivers, the alevins, fry and parr stages living in running water presenting the eel with fish of suitable size, and the habit of the trout of frequenting shallows being favourable to the bottom-living habit of the eel. The depredations of the eels of New Zealand upon trout fry and adults is stressed by Cairns (1941, 1942 *a,b*).

(3) Examination of hundreds of stomachs of trout and young salmon over many years shows that the 'snig' and adult eel are negligible as food for the

salmonids. Hutton (1921) notes that he saw a 12 oz. trout attack an eel 9 in. long; records of such a habit are, however, rare. There is no doubt that trout feed heavily upon elvers during their ascent in spring but the period for this feeding is a short one.

Finally, the points brought out in the preceding paragraphs suggest a policy towards the eel in fishery conservation. In any large lake presenting an association consisting primarily of pike and perch, although the diet of the eel coincides to some extent with that of these fish and the likelihood of the eel preying upon the perch cannot be ignored, there seems little reason to believe that the eel is a detrimental member of such an association. In waters populated primarily by 'coarse' fish (other than pike and perch) it would appear, from a comparison of Hartley's account of the food of such fish in East Anglian waters (1940) with the food of the eel in the Windermere catchment area, that, although the dace (*Leuciscus leuciscus* (L.)), roach (*Rutilus rutilus* (L.)), rudd (*Scardinius erophthalmus* (L.)), bream (*Abramis brama* (L.)), silver bream (*Blicca bjoernka* (L.)) and ruffe (*Acerina cernua* (L.)) feed to some extent on aquatic insect larvae and molluscs, that there would be little probability of serious competition for these foods by inclusion of the eel in a coarse fish community. In any waters conserved for Salmonidae the food requirements of these fish coincide so closely with those of the eel that serious competition between the species may result; this, and the likelihood of the eel being of considerable consequence as a predator on salmon and trout, particularly in running water, but withal of almost negligible value itself as forage for the salmonids, indicate that its presence is undesirable, particularly in running waters.

5. INTERNAL PARASITES

Mention may be made of the parasitic 'worms' which were met with during the investigation. The impression gained during the gut-examinations that very few eels were infested with internal parasites may have been due to unobservance. Nematodes were taken from three eels, a cestode from one and some acanthocephalids from two. The nematodes and cestode were examined by Dr H. A. Baylis of the British Museum (Natural History) and by Miss N. G. Sproston of the Marine Biological Laboratory, Plymouth, to whom I am indebted for their identification. The nematode was *Raphidascaris cristata* (Linstow, 1872) and the cestode *Bothriocephalus claviceps* (Geoze, 1782). Dr H. A. Baylis, of the British Museum (Natural History), informs me that the identity of the species of *Raphidascaris* commonly referred to as *R. acus* (Bloch) is very uncer-

tain, as it is insufficiently described. He has examined some of the material on which Yorke and Maplestone's (1926) figures of '*R. acus*' were based, and believes that it is actually *R. cristata* (Linstow, 1872). Unless Linstow's description of this species is inaccurate, it appears to be distinct from *R. acus*. Dr Baylis recorded *R. acus* and *B. claviceps* from the eels from a Worcestershire pond examined by Hornyold (1922), and also (1939) from eels taken in Hampshire and Berkshire. Acanthocephalids were noted in one eel and recently Miss M. Young of the University of Nottingham, working at Wray Castle on fish parasites, found 15 in one eel, which she identified as *Echinorhynchus truttae* Schrank, 1788, a species already reported by Dr Baylis from English eels. The same worker also found that the lens of the eye of one of the eels was infected with a trematode *Diplostomum* sp.

6. ACKNOWLEDGEMENTS

7. SUMMARY

1. The food of eels (*Anguilla anguilla*) from the Windermere catchment area has been investigated by the examination of the stomach contents of 106 yellow eels from Windermere, 42 from Cunsey Beck and 32 from the River Leven; the food of 60 seaward migrating eels caught in the trap on Cunsey Beck has also been ascertained.

2. Eels feed almost entirely upon bottom-living invertebrates, molluscs predominating in the Windermere fish and the larvae of aquatic insects in those from the Cunsey Beck and River Leven. This distinction is probably due to the size of the eels examined from the two places being different and differences in the faunistic conditions of the two environments.

3. The number of eels from Windermere feeding on fish is negligible; the virtual absence of fish from the diet of Cunsey and Leven eels may be accounted for by the size of those examined.

4. Some seaward migrating eels, including specimens which were changing from the yellow to the silver phase and those which were wholly silver, contained food.

5. The relationship between the feeding habits of the eel and fish associated with it is discussed, some suggestions for fishery policy being based on the discussion.

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COMPETITION AND THE STRUCTURE OF ECOLOGICAL COMMUNITIES

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(With 1 Figure in the Text)

1. AN ANALYSIS OF SOME COMMUNITY SURVEYS

(a) General

If one peruses the lists of species recorded in various ecological surveys of clearly defined habitats, the thing that stands out is the high percentage of genera with only one species present. This is quite a different picture from a faunal list for a whole region or country, in which many large genera are to be found.

There are, of course, theoretical difficulties in deciding exactly what we mean by a clearly defined community or a major habitat, and also considerable practical difficulties during ecological survey work in the field in separating genuine inhabitants from accidental visitors, especially as some of the latter may play a real part in the life of the community. The following analysis is made with clear realization that all community surveys to a certain degree set arbitrary limits to the radiating connexions between species. Such partly arbitrary sections of the larger system of interspersed habitats with their communities will nevertheless show something of the typical structure, without supplying a complete story.

(b) Animal communities

Table 1 gives analyses of fifty-five ecological surveys of animal communities from an extremely wide range of habitats. In three instances some grouping has been adopted to give more reliable figures, which reduces the total to forty-nine units, distributed among twenty-one major types of habitat. The communities cover land, fresh-water, estuary and marine; Arctic, Subarctic, Temperate and one Tropical; free-living and parasitic; and mostly include a very large proportion of the groups of animals present in each habitat.

The percentage of genera with only one species present varies from 69 to 100%, but the greatest frequency is centred round 85%, while about three-quarters of the figures lie between 81 and 95% (Table 2). The corresponding percentage of the number of species belonging to genera in which only one species is present varies more widely, from 46 to 100%. The greatest frequency lies between 71 and 85%, and about three-quarters of the figures lie between 66 and 90% (Table 3).

Genera with four or more species present form a very small fraction of the whole—on the total figures, only 1·32%. In the fifty-five communities, only eleven recorded five or more species in the same genus; while there is only one instance of more than six (in no. 22). These facts are expressed in the figures for the average number of species per genus in each community, which in all instances lies between 1 and 2, the average for the whole lot being 1·38 (range 1·00–1·63). This is shown in another way in Fig. 1, which indicates something like a straight-line relationship between the number of species and number of genera in an animal community.

It is necessary to discuss the validity of the survey data a little, before considering the explanation of these relationships between genera and species:

(1) The range of habitats included is very wide, but it does not contain samples of the most complex habitats, particularly woodland, for the reason that no complete ecological surveys of them have yet been done. Such communities might prove to differ in their structure from those of the simpler kind. This point is discussed again in § 2(b).

(2) There is really no such thing as a uniform habitat, since all habitats consist of interspersed mosaics of micro-habitats or are internally patchy in the distribution of population densities (as with plankton); and since they also are subject to variations in conditions caused by seasonal and other temporal changes. The habitat units chosen as samples have fairly uniform habitat patterns within them, and provide well-established ecosystems that have been studied fairly or very thoroughly by the surveyors.

(3) Few ecological surveys can be complete, yet many of those analysed are undoubtedly very nearly complete within the limitations of the collecting and recording methods used. These limitations usually affect whole groups of organisms, rather than genera within the same family or order, and so do not harm the present analysis. Thus a plankton net will collect all planktonic Crustacea but not any fish; the bottom sampling of benthos may ignore the micro-fauna; the log communities only give the invertebrates, not the

Table 1. *Analysis of genus/species relations in fifty-five animal communities*

General habitat	Community	1 (A)	2	3	4	5	6	+	Total no. of species analysed (B)	Total no. of genera analysed (C)	Average no. of species per genus (B/C)	% of genera with one species present (A/C)	% of 'single species' present (A/B)	Reference
Arctic fjaeldmark	1a Frost-weathered rocky soil, Bear Island	24	2	1	—	—	—	—	31	27	—	—	—	Summerhayes & Elton, 1923, pp. 221–2, 245, 262–3
	1b Rocky Lowland, Prince Charles Foreland, Spitsbergen	13	1	—	—	—	—	—	15	14	—	—	—	
	1c Raised beaches, Klaas Billen Bay, West Spitsbergen	14	8	1	—	—	—	—	33	23	—	—	—	Summerhayes & Elton, 1928, pp. 216–17
	1d Lowland, Reindeer Peninsula, West Spitsbergen	17	5	2	1	—	—	—	42	26	—	—	—	
	Average 1a–d	17	4	1	0·25	0·25	—	—	30·25	22·5	1·35	75	56	
Subarctic fjaeldmark	2 Rocky plateau, Akpatok Island, Ungava Bay, Canada	23	3	—	—	—	—	—	29	26	1·12	88	79	Davis, 1936, p. 321
Arctic heath	3 *Cassiope tetragona* heath, Wijde Bay, West Spitsbergen	21	3	1	—	—	—	—	30	25	1·20	84	70	Summerhayes & Elton, 1928, p. 235
Subarctic heath	4 Better vegetated slopes of ravines, Akpatok Island, Ungava Bay, Canada	26	5	1	—	—	—	—	39	32	1·22	81	67	Davis, 1936, p. 325
	5 Heath (excluding willow scrub), Godthaabsfjord, West Greenland	56	7	1	1	—	—	—	77	65	1·19	86	73	Longstaff, 1932, p. 122
Subarctic scrub	6 Willow (*Salix glauca*) scrub, Godthaabsfjord, West Greenland	34	6	2	2	—	—	—	60	44	1·36	77	57	Longstaff, 1932, p. 126
Temperate grassland	7 Invertebrates of soil and surface vegetation, meadow on clay, near Oxford, England	61	11	2	1	—	—	—	93	75	1·24	81	66	Ford, 1935, p. 198
Temperate woodland	Invertebrates in logs (complete succession, several years), Duke Forest, North Carolina:													Savely, 1939, pp. 377, 381
	8 *Pinus taeda* and *echinata* logs	92	8	1	—	—	—	—	111	101	1·10	91	83	
	9 *Quercus alba, borealis* (=*rubra*), *velutina* and *stellata* logs	118	6	2	—	—	—	—	136	126	1·08	94	87	
Subarctic bog	10 *Eriophorum* bog, Godthaabsfjord West Greenland	17	2	—	—	—	—	—	21	19	1·11	89	81	Longstaff, 1932, p. 131
	11 Bog and pool margins, plateau valley, Akpatok Island, Ungava Bay, Canada	26	3	—	—	—	—	—	32	29	1·10	90	81	Davis, 1936, p. 324
Temperate fresh-water pond	12 General fauna of 8 fresh-water ponds, Bardsey Island, north Wales	21	4	1	—	—	—	—	32	26	1·23	81	66	Pyefinch, 1937, p. 128
	13 Moorland hill pond, rich vegetation, Wales	61	8	1	1	0	1	—	90	72	1·25	85	68	Laurie, 1942, p. 172
Temperate lake benthos	14 Invertebrates, sublittoral, Windermere, English Lake District	38	6	0	1	1	—	—	59	46	1·28	83	64	Humphries, 1936, p. 32
	15 Ditto, profundal	6	1	0	0	1	—	—	13	8	1·63	75	46	Ditto

No. of genera with the following nos. of species present

Table 1 (continued)

General habitat		Community	1 (A)	2	3	4	5	6	+	Total no. of species analysed (B)	Total no. of genera analysed (C)	Average no. of species per genus (B/C)	% of genera with one species present (A/C)	% of 'single species' present (A/B)	Reference
			header: No. of genera with the following nos. of species present												

General habitat	No.	Community	1 (A)	2	3	4	5	6	+	Total no. of species analysed (B)	Total no. of genera analysed (C)	Average no. of species per genus (B/C)	% of genera with one species present (A/C)	% of 'single species' present (A/B)	Reference
Temperate lake benthos	16	Invertebrates, sublittoral 10–40 m., Vättern (cold relict fresh-water lake), Sweden	44	8	1	3	1	1	—	86	58	1·51	76	51	Ekman, 1915, p. 373
Temperate lake, zoo-plankton	17	Lac de Bret, Switzerland, altitude 673 m.	22	3	1	—	—	—	—	31	26	1·19	85	71	Linder, 1904, p. 166
	18	Lake Washington, Washington, near sea-level	18	8	—	—	—	—	—	34	26	1·31	69	53	Scheffer & Robinson, 1939, p. 117
	19	Lake Michigan (Great Lakes):													Eddy, 1927, p. 212
		(a) 1887–8	21	8	1	—	—	—	—	40	30	—	70	52	
		(b) 1926–7	19	6	1	—	—	—	—	34	26	—	73	56	
		Average	20	7	1	—	1	—	—	37	28	1·32	71	54	
Temperate river	20	Invertebrates, River Wharfe, Yorkshire	82	7	6	3	1	1	—	131	99	1·44	83	63	Percival & Whitehead, 1930, p. 296
	21	Invertebrates and fish, River Lark, East Anglia	42	5	1	1	0	1	—	65	50	1·30	84	65	Butcher, Pentelow & Woodley, 1931, p. 103
	22	Invertebrates, fish and Amphibia, River Rheidol, Wales (recovering from lead pollution)	47	6	3	1	0	1	1 (9)	87	59	1·47	80	54	Laurie & Jones, 1938, p. 280
	23	Ditto, River Melindawr, Wales (Stations A–F, lead pollution)	46	4	3	0	1	—	—	68	54	1·26	85	68	Jones, 1940a, p. 193
	24	Ditto, River Dovey, Wales (no pollution)	81	16	5	—	—	—	—	128	102	1·25	79	63	Jones, 1941, p. 18
	25	Invertebrates, River Ystwyth, Wales (zinc pollution; no fish or molluscs)	43	4	1	0	1	—	—	59	49	1·20	88	73	Jones, 1940b, p. 374
Temperate estuary	26	Plankton, River Thames, Southend, 5 years	56	5	3	1	—	—	—	79	65	1·22	86	71	Wells, 1938, p. 116
	27	Benthos and a few plankton invertebrates, and the fish, River Tamar, Devonshire. (Upper salinity at stations, 0·06 ‰–25·3 ‰)	49	4	1	—	—	—	—	60	54	1·11	91	82	Percival, 1929, p. 95
Arctic marine drift-line	28	Intertidal and bottom benthos, River Tay, Scotland	89	5	2	—	—	—	—	105	96	1·19	93	85	Alexander, 1932, p. 37
	29	Invertebrates and birds, Reindeer Peninsula, West Spitsbergen	12	3	1	—	—	—	—	21	16	1·31	75	57	Summerhayes & Elton, 1928, p. 250
Subarctic marine drift-line	30	Invertebrates, Godthaabsfjord, West Greenland	19	2	—	1	—	—	—	23	21	1·10	90	83	Longstaff, 1932, p. 134
Subarctic marine intertidal	31	Invertebrates, Amerdloq Fjord, west Greenland:													Steven, 1938, p. 61
		(a) Rock	14	1	—	—	—	—	—	16	15	—	93	87	
		(b) Sand	5	—	—	—	—	—	—	5	5	—	100	100	
		(c) Mytilus beds	33	2	—	—	—	—	—	37	35	1·06	94	89	
		(a–c) Three types combined	33	2	—	—	—	—	—	37	35	—	94	89	

	No.	Sample													Reference
Temperate marine intertidal	32	Invertebrates, rocky shore, Plymouth, England (4 years after colonization began)	54	3	3	1	1	0	1	73	60	1·22	90	74	Moore & Sproston, 1940, p. 61
	33	Invertebrates and fish, sand shore, Port Erin Bay, Isle of Man	17	—	—	—	—	—	—	17	17	1·00	100	100	Pirrie, Bruce & Moore, 1932, p. 287
	34	Invertebrates and fish, rocky shore (excluding rock-pools), Bardsey Island, Wales	85	10	1	—	—	—	1	108	96	1·12	88	79	Pyefinch, 1943, p. 84
	35	Wharf piles, Wood's Hole, Massachusetts	74	8	3	—	—	—	—	99	85	1·17	87	75	Allee, 1923, pp. 213, 218
Tropical marine intertidal	36	Exposed rocks, ditto	50	4	3	—	—	—	—	67	57	1·18	88	75	Stephenson et al., 1931, p. 44
	37	Coral reef flat, Low Isles, Great Barrier Reef, Australia	50	5	3	—	—	—	—	69	58	1·19	86	72	
Temperate marine benthos	38	Dogger Bank, North Sea, (a) 150 stations [Voyage 48]	38	9	—	—	—	—	—	56	47	1·19	81	68	Davis, 1923, p. 9
	39	Ditto, (b) smaller area (900 sq. miles), 100 stations [Voyages 22, 26, 29]	35	4	—	—	—	—	—	43	39	1·10	90	81	Ditto
	40	Ditto, (c) still smaller area (340 sq. miles), 189 stations [Voyage 39]	29	2	—	—	—	—	—	33	31	1·06	94	88	Ditto
Temperate marine zoo-plankton	41	Shields area, Northumberland, North Sea [Stations 14–30]	39	3	—	•	—	—	—	45	42	1·07	93	87	Savage, 1926, Table 3
Parasite faunas	42	Endoparasites, salamander, *Desmognathus f. fuscus*, stream and swamp-stream margin in woodland, lower Piedmont, North Carolina	13	2	—	—	—	—	—	17	15	1·13	87	76	Rankin, 1937, p. 184
	43	Endoparasites, salamander, *Plethodon cinereus*, oak-hickory forest, above streams, Blue Ridge Mountains, North Carolina	9	1	—	—	—	—	—	11	10	1·10	90	82	Ditto
	44	Ectoparasites, wood-mouse, *Apodemus sylvaticus*, Bagley Wood, Oxford	17	1	1	1	—	—	—	23	19	1·21	89	74	Elton, Ford, Baker & Gardner, 1931, p. 706, etc.
	45	Ditto, endoparasites	16	1	—	—	—	—	—	18	17	1·06	94	89	Ditto, p. 683, etc.
	46	Nest fauna of wild house-mouse (*Mus musculus*) (parasites and other inhabitants), Isle of Lewis, Outer Hebrides	13	2	—	—	—	—	—	17	15	1·13	87	76	Elton, 1934, p. 109
	47	Ecto- and endoparasites of brown rat (*Rattus norvegicus*), England	20	1	1	—	—	—	—	25	22	1·14	91	80	Balfour, 1922, p. 290
	48	Ecto- and endoparasites, steppe ground squirrel (*Citellus pygmaeus*), South-east Russia	23	2	1	—	—	—	—	30	26	1·15	88	77	Sassuchin & Tiflow, 1933, p. 438
	49	Ecto- and endoparasites, cotton-tail (*Sylvilagus floridanus mallurus*), Durham County, North Carolina	10	1	—	—	—	—	1	12	11	1·09	91	83	Harkema, 1936, p. 160
		Totals (49 units)	1912	225	55	17·25	6·25	5	1	2666·25	2221·5	1·38	86	72	
		%	86·07	10·13	2·48	0·78	0·28	0·22	0·04						

birds, etc. But within the groups collected analysis can be made, provided a high proportion of the genera have all their species identified.

(4) It is more important that a number of groups should have been collected completely and separated into reliable species, than that all groups should be recorded. A good many lists that were insufficiently broken down into species had to be omitted. I have, however, accepted certain surveys, mostly fresh-water benthos ones, that record 'species *a*, *b*', etc., without actual Latin names; most of these being immature stages not yet correlated with known adult species. It will be realized, therefore, that the 'total number of species analysed' in Table 1 is seldom the total number present on the area, and is usually a little less than the total number given in the published surveys. Some of the detailed decisions that had to be made are relegated to an Appendix.

Table 2. *Frequency distribution of the percentages of genera with only one species present, in forty-nine animal communities*

Percentage	66–	71–	76–	81–	86–	91–	96–
No.	1	4	4	11	18	10	1

Table 3. *Frequency distribution of the percentages of 'single species' present, in forty-nine animal communities*

Percentage	46–	51–	56–	61–	66–	71–	76–	81–	86–	91–	96–
No.	1	4	3	4	7	9	6	9	5	0	1

(5) Although these communities are treated as if they are a random sample, they do include most of the reliable and fairly complete surveys known to me (except that, in order to retain some balance between different types of habitat, the proportion of European fresh-water surveys is not high). Also, although the percentages are all grouped together into one frequency table (Table 2), it will probably turn out, when enough surveys have accumulated, that some major habitats will show figures consistently higher or lower than the average. At present too few reliable surveys exist to decide whether such differences are really present in the ecosystems concerned, or whether they are inherent in the collecting methods or even in the taxonomic conventions for particular groups.

(c) Plant communities

Only a small sample analysis of plant communities is given here (Table 4), out of the very large published material that exists. No special selection was exercised in the choice of twenty-seven communities for analysis, provided they were complete and on clearly defined habitat areas and the lists were local rather than very large regional ones, except that the samples were intended to cover a wide range of conditions. It is sufficient to prove that the genus/species relationships are similar to those in animal

communities: the frequencies summarized in Table 4 are remarkably similar to those in Table 2, e.g. the average percentage of genera with only one species present is 84 (range 63–96), compared with 86 for animal communities, and the average number of species per genus 1·22 (range 1·06–1·47), compared with 1·38 for animal communities. The almost exact correspondence of these averages may be partly a coincidence, but considering the very wide range of communities analysed, the resemblances are certainly remarkable and would lead one to suppose that there is some common principle operating both for plants and animals. The agreement is important also because most plant ecological surveys are more complete than animal ones, and because we know by direct evidence something of the direct competition that exists between plant species.

2. DISCUSSION AND WORKING HYPOTHESIS

(a) Faunal statistics

One possible explanation of the statistical relationships described above would be that the frequencies of species in genera simply reflect those of the fauna as a whole. For if, say, 86 % of species in the British Isles belonged to genera of which only one species was present in this region, the figures in Tables 1 and 4 would be the record of a faunistic distribution, rather than of any peculiarity of homogeneous communities taken separately. Since insects form a high proportion of the fauna on land and in fresh water, we can take the British insect fauna as a test of this question, using the recently published 'Check list of British insects' (Kloet & Hincks, 1945), in which the numbers of established genera and species are summarized for each order (or in some cases, suborder). In Table 5 these thirty-one insect groups are arranged in ascending series of size, the Hemiptera being split into four, the Hymenoptera into six, and the Diptera into two subgroups. The frequencies for different groups are given in Table 6, with those of the animal communities for comparison. Whereas all the community figures for the number of species per genus lie in the frequency class 1·00– (actually, 1·00–1·63), only about 10 % of those for the insect groups are in that class, and their percentages range from this to over 7·00. Although the greatest frequencies lie in the classes 2·00– to 4·00–, with a peak in 2·00–, the weight of the very large insect groups Hymenoptera, Lepidoptera, Diptera and Coleoptera (which together form 84 % of the total British insect

species and which all have high ratios) brings the average for the whole assemblage of insect groups to 4·23.

Since Kloet & Hincks seem to have inclined rather strongly towards the splitting of genera (i.e. calling subgenera genera) and the ecological surveys analysed here were done at earlier periods when generic splitting in most groups had gone less far, it may safely be stated that, *on the average*, for every species of insect present in a British animal community there are at least three or four others of the same genus for the eleven largest groups, the percentages being given in the fourth column of Table 5. They range from 28 to 57 %, but most of them lie between 44 and 57 %, and the average for the whole lot is 50 %. This is the figure that we may compare with 86 % for the animal communities. The differences between particular communities and the fauna as a whole are evidently considerable in this respect, whether we consider the average number of species per genus or the percentage of genera with 'single species'. The difference is greater for the former figure than for
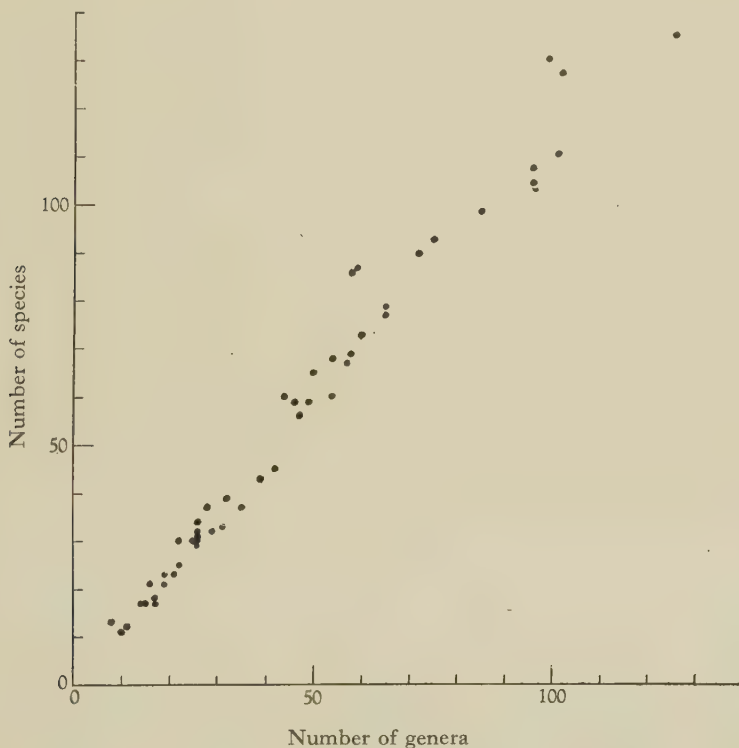
Fig. 1. Relation between the number of species and the number of genera present in forty-nine animal communities (from Table 1).

present in the country. But in the communities considered, the average number of species per genus was only 1·38, i.e. *on the average* every species only had two-fifths of another species living with it. This comparison is not quite satisfactory, because the insect statistics refer only to the insect groups of a fairly typical temperate continental island, while the community figures are derived from a very wide sample of varied animal groups from habitats in the Northern Hemisphere; but I think it illustrates a real difference that will be generally found to occur.

The Check List does not summarize the numbers of monospecific genera. I have therefore done this

the latter, owing to the presence in the general faunal lists of a great many large genera, with numbers far exceeding the usual limit of three or four found in the community lists.

It can still be said that the community statistics might be reflecting the general fauna picture for a smaller region within a country. I have considered making a further check by analysing the lists of county faunas, such as those published in the *Victoria County Histories*, but came to the conclusion that the comparison would probably be meaningless, because these lists are compiled over a very long period of time and do not necessarily describe the fauna of

Table 4. *Analysis of genus/species relations in twenty-seven plant communities*

General habitat	Community	No. of genera with the following nos. of species present							Total no. of species analysed (B)	Total no. of genera analysed (C)	Average no. of species per genus (B/C)	% of genera with one species present (A/C)	% of 'single species' present (A/B)	Reference
		1 (A)	2	3	4	5	6	+						
Arctic fjaeldmark	1 Frost-weathered rocky soil, Bear Island	16	4	1	1	—	·	—	31	22	1·41	73	52	Summerhayes & Elton, 1923, p. 220
	2 Rocky lowland (non-polygon soil), Prince Charles Foreland, Spitsbergen	24	5	3	—	—	—	—	43	32	1·34	75	56	Ditto, p. 244
Arctic heath	3 *Cassiope tetragona* heath, Wijde Bay, West Spitsbergen	28	7	0	1	1	?	—	51	37	1·38	76	55	Summerhayes & Elton, 1928, p. 233
Subarctic heath	4 *Empetrum–Betula nana* heath, Billefjordelv area, Finmark, Norway	26	3	2	1	—	—	—	42	32	1·28	81	62	Leach & Polunin, 1932, p. 420
Subarctic woodland	5 Drier *Betula odorata* forest, same area as (4)	24	1	1	—	—	—	|	29	26	1·12	92	83	Ditto, p. 417
Temperate grassland	6 Nardetum, Cader Idris, north Wales	20	3	—	—	—	—	—	26	23	1·13	87	77	Evans, 1932, p. 25
	7 *Deschampsia flexuosa* grass heath, Bunter sandstone, Nottinghamshire, England	42	10	1	0	1	—	—	70	54	1·30	78	60	Hopkinson, 1927, p. 159
	8 Primitive chalk grassland, Buriton, West Sussex, England	52	10	2	1	—	—	·	82	65	1·26	80	63	Tansley & Adamson, 1925, p. 185
Steppe	9 *Avena desertorum* meadow steppe, Kuznetszk District, Saratov, Russia	46	8	2	—	—	—	—	68	56	1·21	82	68	Keller, 1927, p. 220
Temperate scrub	10 Limestone heath-scrub, Ballyvaghan, Co. Clare, Ireland	25	0	1	—	—	—	—	28	26	1·08	96	89	Tansley, 1939, p. 474
Temperate carr	11 Open carr, Esthwaite Fens, Lake District, England	50	5	2	0	0	0	1 (7)	73	58	1·26	86	68	Pearsall, 1918, p. 61, summarized by Tansley, 1939, p. 644
	12 Valley fenwoods, River Lark, East Anglia, England	35	5	3	1	—	—	—	58	44	1·32	80	60	Farrow, 1915, p. 226, summarized by Tansley, 1939, p. 467
	13 Coppiced alder carr, Cothill, Berkshire, England	38	4	0	1	—	—	—	50	43	1·16	90	76	Tansley, 1939, p. 469
	14 Alder carr, Wheatfen Broad, Norfolk, England	47	9	1	1	—	—	—	72	58	1·24	81	65	Ellis, 1935, summarized by Tansley, 1939, p. 461

No.	Category	Locality / description				Genera	Species	1	2	3	4	5	6	7	Reference
15	Temperate woodland	Ashwood, Ling Ghyll, Yorkshire, England	69	83	1·20	60	72	50	8	2	—	—	—	—	Tansley, 1939, p. 433
16		Highland oakwood, Glenmore, Scotland: (a) Portclair (*Quercus robur*)	83	90	1·10	42	46	38	4	—	—	—	—	—	Ditto, p. 344
17		(b) Loch Leven (*Q. sessiliflora*)	89	94	1·06	52	55	49	3	—	—	—	—	—	
18		Birchwood, Cader Idris, north Wales, 800–1100 ft.	80	89	1·11	45	50	40	5	—	—	—	—	—	Evans, 1932, p. 20
19		Mature beechwood (sere 1, stage 3), Singleton Forest, Sussex Downs, England	87	93	1·07	42	45	39	3	—	—	—	—	—	Watt, 1925, p. 50
20		Red fir forest, Sierra Nevada, California	64	80	1·24	75	93	60	12	3	—	—	—	—	Oosting & Billings, 1943, p. 271
21	Temperate lake plankton	Windermere, England	75	90	1·20	20	24	18	1	0	1	—	—	—	Pearsall, 1932, p. 261
22	Temperate lake littoral	Phanerogams, Lake Mendota, Wisconsin	62	87	1·40	15	21	13	1	0	0	0	1	—	Denniston, 1921, p. 500
23	Subarctic marine intertidal	Amerdloq Fjord, West Greenland	83	91	1·09	11	12	10	1	—	—	—	—	—	Steven, 1938, p. 62
24	Temperate marine intertidal	Rocky shore, Plymouth, England (4 years after colonization)	86	92	1·08	13	14	12	1	—	—	—	—	—	Moore & Sproston, 1940, p. 319
25	Tropical marine intertidal	Coral reef flat, Low Isles, Great Barrier Reef, Australia	43	63	1·47	19	28	12	5	2	—	—	—	—	Stephenson *et al.*, 1931, p. 45
26	Marine phytoplankton	Aberystwyth Harbour, Wales	78	90	1·15	20	23	18	1	1	—	—	—	—	Lloyd, 1925, p. 103
27		Shields Area, Northumberland, North Sea [Station 26]	54	78	1·45	9	13	7	1	0	1	—	—	—	Savage, 1926
		Totals (27 units)	69	84	1·22	999	1219	839	120	27	9	2	1	1	
		%						83·99	12·01	2·70	0·90	0·20	0·10	0·10	

a region in one year or a short period of years; whereas the community surveys are done usually within a year or at most a few years. Nevertheless, the faunal list does indicate the species that either live or have attempted to live within the area, and it is notable that 54 % of the British species of Hemiptera Heteroptera have been recorded from an area as small as the county of Oxfordshire (China, 1939) and

conclusions drawn here. But although the list of habitats is an extremely varied one and gives a very wide sampling, it is deficient (except for no. 7, Table 1) in one very important class of animal community, that of terrestrial habitats of temperate and tropical regions containing complex plant associations. The reason for this omission is, of course, the absence of sufficiently complete surveys hitherto.

Table 5. *Relation between the number of genera and of species in thirty-one British insect orders or suborders (established species), columns 1 and 2 from Kloet & Hincks (1945)*

Order	No. of species	No. of genera	No. of species per genus	% of genera with only one species present
Mecoptera	4	2	2·00	—
Megaloptera	6	3	2·00	—
Dermaptera	9	7	1·29	—
Protura	17	4	4·25	—
Strepsiptera	17	5	3·40	—
Thysanura	23	7	3·29	—
Plecoptera	32	15	2·13	—
Orthoptera	38	27	1·41	—
Odonata	42	21	2·00	—
Ephemeroptera	46	19	2·42	—
Siphonaptera	47	24	1·96	—
Neuroptera	54	18	3·00	—
Psocoptera	68	33	2·06	—
Hemiptera, Coccoidea	103	38	2·71	—
Thysanoptera	183	42	4·35	—
Trichoptera	188	70	2·69	—
Hymenoptera, Cynipoidea	228	49	4·65	—
Collembola	261	62	4·21	—
Anoplura (including Mallophaga)	286	73	3·92	—
Hemiptera, Aphidoidea	375	122	3·07	—
Hymenoptera, Symphyta	430	92	4·67	35
Hemiptera, Homoptera	434	92	4·71	46
Hemiptera, Heteroptera	499	221	2·26	57
Hymenoptera, Aculeata	531	139	2·82	44
Hymenoptera, Proctotrupoidea	613	93	6·60	28
Hymenoptera, Chalcidoidea	1564	214	7·31	51
Diptera, Cyclorrhapha	2072	652	3·18	53
Lepidoptera	2187	657	3·33	57
Hymenoptera, Ichneumonoidea	2825	485	5·82	44
Diptera, Orthorrhapha	3127	480	6·53	45
Coleoptera	3690	947	3·90	50
Total insects*	19999	4713	4·23	
Average (from raw totals, 11 groups)				50

* Omitting 25 'Addenda' to the list.

that Waters (1929) found that at least 58 % of the British species of micro-Lepidoptera had been recorded within seven to ten miles of Oxford.

(b) Limitations of the community data

It was pointed out in § 1 that the community surveys analysed are certainly incomplete in many respects, but that the features in which they themselves were lacking were not likely to invalidate the

On the whole, the list given in Table 1 contains animal communities in which the species live on a comparatively few different basic sources of food. This applies to log-dwelling herbivores, which depend on phloem, on fungi growing in the galleries made by the phloem-eaters, and on the wood (Savely, 1939); to soil animals; to fresh-water, estuarine and marine bottom detritus or plankton feeders; to intertidal animals dependent on plankton; to zooplankton

itself; to drift-line animals eating decaying matter; and to blood-sucking ectoparasites. I do not mean that there is no ecological differentiation in the food habits of species living, say on phloem in logs or mud on the sea bottom; only that this type of community consists mainly of a few ecological groups each broadly drawing upon the same natural resources for its basic food, with of course the usual predator-parasite food cycle rising from it.

Even in those aquatic habitats that have a number of plant species (e.g. fresh-water benthic phanerogams, intertidal sea-weeds, and phytoplankton) few of the herbivores seem to be restricted to one or a few plant species. The same thing applies in general to Arctic and Subarctic terrestrial communities, where specialization of herbivores is rather exceptional.

mostly species pairs—also show strong ecological differences in habits, although they live within the same community. Lack's study (1944) of passerine birds has brought this point out especially clearly. He also gives many instances of genera whose species are split up between different major habitats. In other instances, although we have not yet got any direct evidence of different habits or tolerance ranges, quantitative survey shows one species of a pair to be much more abundant than another. Thus in his Dogger Bank samples Davis (1923, Voyage 48) got 1182 specimens of the lamellibranch *Spisula subtruncata*, and only four of *S. solida*. These appear, however, as a species pair in Table 1 of the present paper. Undoubtedly some other 'species pairs' will be due to chance immigration of one species not living in that habitat, but these (as also instances of

Table 6. *Frequency distributions of numbers of species per genus in (a) forty-nine animal communities (b) thirty-one British insect orders or suborders*

	1·00–	2·00–	3·00–	4·00–	5·00–	6·00–	7·00–
No. of communities	49	—	—	—	—	—	—
% of communities	100	—	—	—	—	—	—
No. of orders or suborders	3	10	8	6	1	2	1
% of orders or suborders	9·7	32·3	25·8	19·4	3·2	6·4	3·2

The situation in highly organized terrestrial communities like heath, meadow, scrub and woodland is different. Here we find large numbers of monophagous species, especially among insects, attached to particular plant species. Since there may be commonly up to seventy species of plants in one association, the majority of which are phanerogams edible to some animals, the possibilities for ecological differentiation within the community are therefore much greater than in communities of the type so far surveyed with any completeness. Such terrestrial communities do not cover a larger area of the globe than ones of the simpler trophic type, but they do contain some of the most highly organized and complicated relationships known between species, and I wish to make it quite clear that the conclusions that follow should be treated as an approach to the more complex problem, through the evidence for simpler communities that has already been accumulated in the short time that animal ecology has been a science.

(c) Ecotypic differentiation

It is already well known that ecotypic differentiation occurs between many species of the same genus. What this community analysis shows is that the amount of differentiation is apparently very high, and that it is a prominent feature of all the communities for which we have sufficient knowledge to make the analysis. There is no doubt that some of the 14 % of genera that have more than one species present—

temporary establishment) might also apply to the single species, and we cannot therefore make any statistical proviso from them. It can be concluded that the amount of ecotypic differentiation in genera is really very high in communities of the type we are considering here, and that it is the exception to find groups of species of the same genus occupying the same ecological niche on the same area or apparently doing so (as does, however, occur in genera like the lamellibranch *Pisidium* or the larvae of the black-fly *Simulium* in fresh water).

(d) Competition and community structure

Ecological research has discovered a good deal about the 'vertical' organization of animal communities. By 'vertical' I mean here, not vertical layering of the habitat, but the flow of matter and energy through different levels of consumption, as found in food chains, with their herbivore-plant, predator-prey, parasite-host and other relationships; fluctuating equilibrium between the stages in these chains; cover, making such equilibrium possible; daily and other activity rhythms causing alternating mass action of different components of the community in response to environmental cycles; and the ultimate limit (usually about five stages) set to the number of consumer levels by the size relations of animals and the pyramid of numbers. In this field of ecology it is possible to proceed with some general measure of agreement on the fundamental principles at work

(see Lindeman, 1942, who has restated the subject in a useful essay).

We also have a great deal of information, though none of it complete in respect to any single species, about the tolerance ranges, optima and preferenda that animals have in regard to various habitat factors like temperature, humidity and amount and quality of food—the ranges, etc. often varying with the sex and life history stage of the species and with the type of life process (growth, viability, reproduction, activity, etc.) studied. Here again, research is progressing along well-defined lines, though still very weak upon the fundamental problem of habitat selection in nature.

When we come to the 'horizontal' organization of animal communities, i.e. the dynamic relations between species of the same consumer level, we find that little is known except from very simplified laboratory experiments and from certain lines of *a priori* reasoning. The pros and cons of argument on this question were partly explored in the British Ecological Society's Symposium (21 March 1944) on 'The ecology of closely allied species' (Anon. 1944), at which the substance of the present paper was put forward for discussion. But that discussion was mainly concerned with closely allied forms, whereas I wish to consider now the relation between all species of the same genus. The statistics of Table 1, and the field lists on which they are based, really mean that these animal communities have, at each level of consumption (i.e. food-chain stages 1, 2, 3, 4,...) a certain number, from several to a score or more, of species that mainly belong to separate genera. These, as has been indicated, could be broken up into subgroups each drawing its food from a common pool, though not necessarily from exactly the same part of it at the same time, or in the same way.

We simply do not understand exactly why populations of, say, a Pentatomid bug, a grasshopper, a moth caterpillar, a vole, a rabbit and an ungulate should be able to draw upon the same common resource (grassland vegetation) and yet remain in equilibrium at any rate sufficiently to form a stable animal community over long periods of years. In all communities the primary resources of plant or decaying matter (or with parasites, tissues or the food of the host) are split up in this way between a number of species, each of which is able to maintain, though with fluctuating equilibrium, its own share of the common natural resource. I think it has usually been assumed, by analogy with the specific food habits of monophagous or not very polyphagous insects, that the equilibrium is made possible by some specialized division of labour, and that the animals do not come into direct competition at all; or else that the amount of resources is generally sufficient to provide for all

the populations present because they are limited by factors other than food in the increase of their populations. The second idea is on the whole supported by the general evidence that animals do not normally become limited in numbers by starvation, and that the biomass of phanerogamic vegetation is far beyond that of animals dependent on it. However this may be, we know extremely little about the whole subject.

Darwin, in *The Origin of Species*, remarked that 'As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera. We see this in the recent extension over parts of the United States of one species of swallow having caused the decrease of another species. The recent increase of the missel-thrush in parts of Scotland has caused the decrease of the song-thrush. How frequently we hear of one species of rat taking the place of another species under the most different climates! In Russia the small Asiatic cockroach has everywhere driven before it its great congener. One species of charlock will supplant another, and so in other cases. We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature; but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life.'

More recently, Gause (1934) and other laboratory workers have shown by experiments in controlled environments how one of two similar species of a genus introduced into a culture will prevail eventually over the other. That this type of competition is not confined to species of the same genus is well proved by the experiments of Crombie (1945, 1946) with grain insects, in which a beetle was able eventually to crowd out a moth, both having larvae living inside the grains of wheat; also in similar experiments with beetles by Park, Gregg & Lutherman (1941). Here competition was effective between members of two different orders of insects, and we have the type of equilibrium problem that is most commonly encountered in the field. The importance of the community analysis given in the present paper is that it confirms the general proposition that some (though not necessarily all) genera of the same consumer level that are capable of living in a particular habitat at all can coexist permanently on an area; whereas it is unusual, in the communities analysed, for species of the same genus to coexist there. We therefore arrive at some points for a working hypothesis to cover our present limited knowledge of competition in relation to basic community structure.

It should be stressed that 'competition' is here used not merely for direct antagonism or struggles for space, etc., but as an objective description (in the same way that 'natural selection' or the 'struggle for existence' are only shorthand terms) of the interplay of longevity and fertility factors of all kinds (known and unknown) favouring one species at the expense of another.

(1) Every habitat that supports a whole community of animal species contains one or more pools of natural resources available for the building up of animal populations, plant resources (alive or dead) being usually the most immediately important, and in all cases the ultimate source there or elsewhere.

(2) In habitats where there are not large numbers of terrestrial plant species suitable for food specialization by animals (i.e. most of those considered in Table 1), these resources are exploited for the greater part by genera with only one species present on that area of habitat, genera with more than two species present forming a small fraction only. Very large genera do not seem to be represented in full force at all. The main extra-specific ecological relations in such communities are between organisms with generic differences.

(3) We do know a little, experimentally and from field observations (especially on introduced species and their allies) about the effectiveness of competition between species of the same genus. We also know that similarly effective competition can occur between species of separate genera, or even orders. We do not at present know what maintains the state of equilibrium between the different genera actually found in the natural communities analysed, but must postulate that there is some ecological condition that buffers or cuts down the effectiveness of competition between species separated by generic characters. This problem is therefore seen to be the central problem in animal community structure, because it is the variety of species that can coexist at the primary consumer level, that makes possible the considerable complexity of the superstructure of secondary and other consumers.

(4) The comparative shortness of the lists in the community surveys analysed suggests that on any one area of a given habitat, there is in fact restriction upon the number of primary consumers that can coexist (see Elton, 1933), and that there is therefore also some real state of population competition or tension between the different primary consumers, just as there is known to be between primary producers in plant communities.

There is a point about competition that has perhaps not yet been brought out clearly in this discussion. It does not follow that because we find only one species of a certain genus living in a particular animal community on a particular area, that this is the only species of that genus that is capable of living in that habitat. In other words, we have to distinguish carefully between ability to live in a habitat and ability to live among a particular assemblage of other species present there. There may be lists of species, though usually short ones, of the same genus, all capable of contending with the habitat conditions (tundra, marine intertidal, etc.), but it may still be true that only one (or not often more than two) of them can coexist permanently on the same area of it. So we might not be surprised to find a given niche occupied in one area by one species and in another area of the same general habitat by another. Such differences in distribution might either be due to minor variations in the habitat that we have perhaps not yet detected, or they might be due to the process of competition that has been postulated.

The laboratory experiments of Park et al. (1941) illustrate the working of such a situation between two species of beetles, *Tribolium confusum* and *Gnathocerus cornutus* of the same family Tenebrionidae, competing for a common food supply of ground cereals and yeast, but each cannibalizing the early stages of the other species. Competition was well marked between these two species, but the end result depended partly upon the relative initial densities of the two forms. It was possible to get pure or almost pure cultures of either species developing from cultures that had been initially mixed. In nature we might expect to find a number of instances of this happening between species of the same genus, although all the species concerned might be found in some area or other of the general habitat under observation. In discussing the statistical picture of communities given in the present paper, it is therefore essential to remember that each survey was made on a relatively (though not always absolutely) small area of the total habitat.

Finally, something must be said about current trends in taxonomic methods, and especially about fashions for lumping or splitting genera, for these will have a good deal of influence in future handling of community statistics of the type we have been considering. Practically all the animal surveys in Table 1 were done in the 20 years 1921–40, and their nomenclature is a random sample of the taxonomic practices, fashions, advances and retreats, and equilibria of group specialists in various countries during that period and before it. No doubt a good deal of the differences in the frequency pictures for different surveys can be attributed to these variations in taxonomic treatment. Future comparisons will have to take into account the marked tendency for further splitting of genera in many groups of animals, and in some plants, with the reduction in average numbers of species per genus that this involves, and increase

in number (though not always necessarily in the percentage) of monotypic genera. I believe that further research on community structure will eventually give us some new, ecological, criteria for generic classification.

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4. SUMMARY

1. Analysis was made of the published ecological surveys of fifty-five animal (including some parasite) communities and twenty-seven plant communities from a wide range of habitats, and the frequencies of genera with different numbers of species tabulated. A rather constant and high percentage of genera with only one species present was found, the average being 86 % for animal and 84 % for plant communities. The corresponding average numbers of species per genus were 1·38 and 1·22.

2. These figures differ considerably from those of a faunal list for any large region, e.g. the percentage of genera with only one species present for eleven large British insect groups is 50, and the average number of species per genus for all British insects is 4·23.

3. The difference in species/genus frequencies between ecological surveys of relatively small parts of any general habitat, and those for faunal lists from larger regions, is attributed to existing or historical effects of competition between species of the same genus, resulting in a strong tendency for the species of any genus to be distributed as ecotypes in different habitats, or if not, to be unable to coexist permanently on the same area of the same habitat.

4. These conclusions apply at present only to the list of communities hitherto surveyed with any completeness, which does not include a sufficient sample of terrestrial habitats like heath, meadow, scrub and woodland containing many plant species. The animal communities analysed are mostly ones in which the primary consumer species depend on only a few natural resources.

5. The ability of certain groups of species, mostly separated by generic characters, to exist together on the same area while drawing upon a common pool of resources, is one of the central unsolved problems in animal community structure and population dynamics.

APPENDIX

Special notes on the compilation of Table 1

Commu-
nity no.

1–11 Insect parasites omitted from the table.

1–6 Immigrant adult aquatic flies are included because they are an integral part of the food supply of spiders on land. A part of the micro-fauna of mites and Collembola has probably been omitted from all these surveys, as it requires special methods of collection (see Hammer, 1944).

8–9 Mites omitted from the table.

11 Subgenera of *Spaniotoma* treated as separate genera, for uniformity with other surveys.

12 Entomostraca omitted from the table, also five records from an earlier survey.

14–15 All Chironomidae genera containing any species just marked 'sp.' or 'gr.' (for group) omitted from the table.

16 The depth taken for sublittoral is slightly arbitrary, as the actual limits vary in different parts

Commu-
nity no.

of a lake. Chironomidae and most Trichoptera omitted from the table.

19 Two independent surveys of Lake Michigan were done 40 years apart. There were some significant differences in species, but little in the genera present.

20 Chironomidae omitted from the table.

22–23 Diptera omitted from the table.

26 Fish omitted from the table.

35–36 Surveys covered 9 years.

38–40 This survey does not include all bottom-living fish.

41 Autotrophic flagellates omitted from the table.

45–47 Spirochaetes and bacteria omitted from the table.

48 Single records omitted from the table.

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THE DISTRIBUTION OF SPIDERS AND MITES UP TO 300 FT. IN THE AIR*

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(With 3 Figures in the Text)

1. INTRODUCTION AND ACKNOWLEDGEMENTS

In the course of an investigation primarily concerned with the aerial drift of insects (Freeman, 1945), a number of spiders and mites were captured. The collections were made, over a mile front, by nets, 1 yd. in diameter, flown at heights of 277, 177 and 10 ft., from three of the masts of the Beam Wireless Station at Tetney, Lincolnshire, during 1934 and from March to November in 1935.

spiders in one million cubic feet of air), and the number of species increased from June onwards, being at a maximum in August and September and showing a tendency to increase again from the beginning of October onwards (Fig. 1, Table 2). The average population densities at each height were fairly equal, that at 177 ft. being the maximum.

The commonest family in numbers (84) and in species (11) was the Linyphiidae: of the number, 58 were immature forms and all the adults except three

Table 1. *The number of species (in brackets) and individuals of each family and the average density of population of spiders at each height*

| Family | Height | | | | |
	277 ft.	177 ft.	10 ft.	Total	As %
Linyphiidae	24 (6)	45 (8)	15 (7)	84 (11)	62·6
Lycosidae	2 (1)	3 (2)	1	6 (3)	4·5
Thomisidae	1	3 (1)	2 (1)	6 (1)	4·5
Argiopidae	3 (1)	1	0	4 (1)	3·0
Tetragnathidae	2 (2)	1 (1)	0	3 (2)	2·2
Theridiidae	0	1	0	1 (1)	0·8
Unidentified	14	6	10	30	22·4
Total	46 (14)	60 (16)	28 (10)	134 (20)	100
Total (immature stages only)	22 (4)	44 (4)	10 (1)	76 (8)	
Average population density	0·5	0·8	0·7		

The work was carried out under the direction of Prof. A. C. Hardy, to whom I am indebted for much help and criticism. My thanks are due to Cables and Wireless Ltd., whose co-operation enabled the work to be carried out, and to Mr W. S. Bristowe for kindly undertaking the determination of the spiders collected.

2. GENERAL ACCOUNT OF THE SPIDERS COLLECTED

Of the 134 individuals and 20 species, 106 and 17 respectively were taken above ground-level (Table 1), only three species being confined to that level. The 'density of population' (defined as the number of

Table 2. *The average monthly population densities of spiders at each height and the means for the whole period*

Month	277 ft.	177 ft.	10 ft.
Mar.	0·1	0	0
May	0	0·3	0·4
June	0·3	0	0·6
July	0·9	0·8	0·3
Aug.	0·9	2·0	2·0
Sept.	0·6	0·9	0·7
Oct.	0·1	0·8	0·3
Whole period	0·5	0·8	0·7

were included in this family (Tables 1, 3). Of the other families only three species were adults (three individuals only), the remaining 47 individuals being immature. None of the adult Linyphiidae, with the exception of an *Erigone* sp., were taken before July.

The general nature of the aerial fauna of spiders is in agreement with the observations of Bristowe (1929, 1939–41), who states that the young of most

spiders and the adults and young of the Linyphiidae disperse themselves by wind. Of the nine spiders observed by Bristowe (1939–41, p. 191) as being the most common aeronauts, seven were taken in the present collections: *Erigone dentipalpis*, *E. atra*, *Bathyphantes gracilis*, *Meioneta rurestris*, *Lepthyphantes tenuis* and *Savignia frontata* (Table 2).

from *H* to *h*. One may thus generalize by stating that the maximum numbers of spiders may be expected in the air when the air temperature is more than 64° F., the relative humidity is less than 60%, and the wind velocity does not exceed 12 m.p.h. It would appear that the wind velocity is the main controlling factor, and the relation between wind

Table 3. *The number of individuals of spiders and mites taken at each height sampled and the months in which they occurred*

Name	Months	277 ft.	177 ft.	10 ft.	Total
LINYPHIIDAE					
Immature forms	6 7 8 9 10 11	15 (7)	36 (11)	7 (6)	58 (15)
Erigone atra Bl.	7 8	3 (2)	1	1	5 (3)
Meioneta rurestris C. L. Koch	7 . 9 10	2	1	1	4 (4)
Savignia frontata Bl.	7 8 . 10	1	2 (2)	1	4 (3)
Lepthyphantes sp.	8 9	1	1	1	3 (3)
L. tenuis Bl.	9 10 11	1	1	1	3 (3)
Erigone dentipalpis Wid.	7 . 9	0	0	2	2 (2)
Erigone sp.	6	0	0	1	1
Centromerus concinnus Thor.	11	0	1	0	1
Bathyphantes gracilis Bl.	7	0	1	0	1
Bathyphantes sp.	8	0	1	0	1
Porhomma micropthalmum Cambr.	9	1	0	0	1
LYCOSIDAE					
Lycosa sp. (immature)	7 . 9	1	1	0	2 (2)
Immature forms	8	1	1	0	2 (1)
Tarentula sp. (immature)	8	0	1	0	1
Trochosa terricola Thor. (immature)	8	0	1	0	1
TETRAGNATHIDAE					
Pachygnatha sp.	8	0	1	0	1
P. listeri Sund.	9	1	0	0	1
Tetragnatha extensa L. (immature)	9	1	0	0	1
ARGIOPIDAE					
Aranea sp. (immature)	9 10	2 (2)	1	0	3 (2)
A. sexpunctata L. (*umbratica* Clerck.)	6	1	0	0	1
THERIDIIDAE (immature)	11	0	1	0	1
THOMISIDAE					
Xysticus viaticus L. (immature) (*cristatus* Clerck.)	8 9 10	1	3 (2)	2 (2)	6 (5)
UNDETERMINED	5 6 7 8 9 10 11	14 (7)	6 (6)	10 (5)	30 (12)
ACARINA (undetermined)	3 5 6 7 8 9 10	3 (3)	14 (5)	140 (13)	157 (13)

No. of individuals and occurrences (in brackets)*

* The total number of possible occurrences was 31 at each height.

3. THE INFLUENCE OF WEATHER CONDITIONS ON THE NUMBER OF SPIDERS IN THE AIR

The effect of temperature, humidity and wind velocity on the numbers of spiders in the air at each height sampled is shown in Fig. 2 and Table 4, where each pair of factors is considered in combination. For each factor the dividing line was drawn so that there were approximately equal numbers of observations in each range (Table 5).

It is clear that the population density at all heights increases markedly from *W* to *w* and from *t* to *T*, although the latter is not so clear at high humidities. The effect of humidity is not so well marked, although there is a tendency for increase

Table 4. *The relation between density of spider population and temperature, humidity and wind velocity considered in combination* (see Fig. 2)

Range		277 ft.	177 ft.	10 ft.
Temperature and humidity (C)	*tH*	0·2	0·4	0·5
	TH	0·5	0·5	0·4
	Th	1·4	1·9	1·5
	th	0·1	0·6	0·3
Humidity and wind velocity (A)	*wH*	0·5	0·9	0·6
	WH	0·2	0·1	0·3
	Wh	0·1	0·2	0·2
	wh	1·2	2·1	1·4
Temperature and wind velocity (B)	*tW*	0·1	0·1	0·2
	TW	0·3	Nil	0·4
	Tw	1·4	2·0	1·4
	tw	0·3	1·1	0·7

velocity and the population density is shown in Fig. 3 and Table 6, from which it is seen that the maximum population densities at all heights were recorded at the lowest wind velocity and that there is a marked falling off with increase of wind velocity.

These observations are in agreement with those of Bristowe (1929) in regard to wind velocity, but not in regard to humidity. He states that the ideal conditions to produce the urge to migrate in Liny-phiidae are 'still sunny days in spring, autumn and early summer when humidity is high'.

Table 5. *The ranges of temperature, humidity and wind velocity*

Factor		No. of observa-tions	Range
Temperature	Higher (T)	13	64–83° F.
	Lower (t)	15	43–64° F.
Humidity	Higher (H)	13	60–73 % R.H.
	Lower (h)	15	37–59 % R.H.
Wind velocity	Higher (W)	17	14–35 m.p.h.
	Lower (w)	14	6–12 m.p.h.
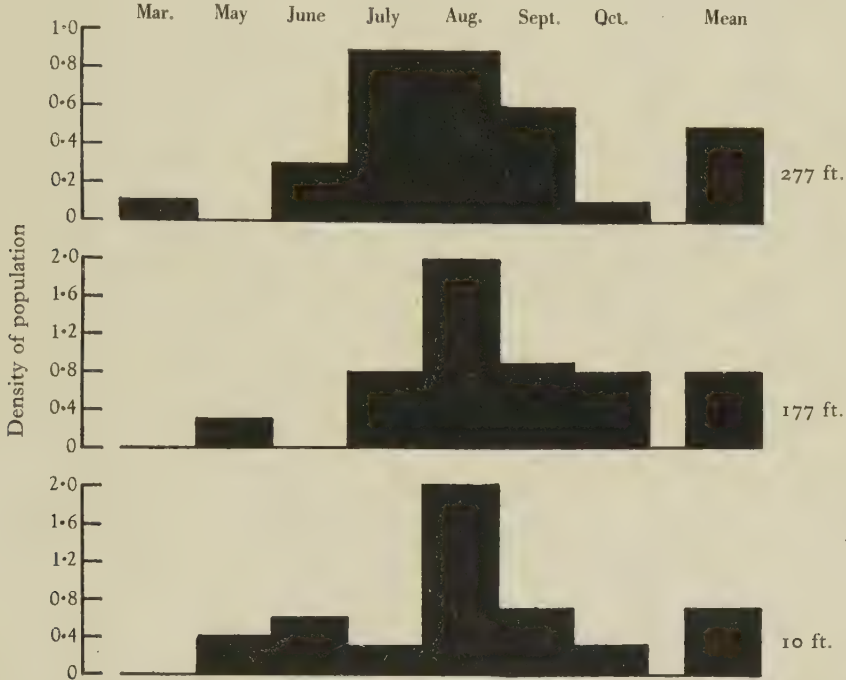
Fig. 1. The average monthly population densities of Araneida at each height and the means for the whole period. (Vertical scale of top figure twice that of the lower two.)

4. VARIATION OF POPULATION DENSITY ACCORDING TO THE DIRECTION OF THE WIND

The greatest density of population occurred when the wind was from the north-east.

The North Sea lies only 1½–2 miles to the east of the wireless masts, and thus an easterly wind only traversed that distance over the land before reaching the nets. It is possible that all the spiders taken on days of easterly drift had been derived from the land to the east of the masts, but the capture of spiders over the North Sea (Hardy & Milne, 1937) lends support to the possibility that some, at least, may have been carried in from over the sea.

Table 6. *The relation between wind velocity and density of spider population*

Range (m.p.h.)	Mean (m.p.h.)	277 ft.	177 ft.	10 ft.
6– 9	8	1·5	2·7	1·7
10–12	11	0·5	0·7	0·7
14–21	18	0·1	0·1	0·4
22–25	23	0·1	0·2	0·2
35	35	0·0	0·0	0·5

5. DISCUSSION

The evidence for the dispersal of spiders by air currents is fully discussed by Bristowe (1929, 1939–41, pp. 182–201). Most of the observations have been made at or near ground-level and refer to spiders
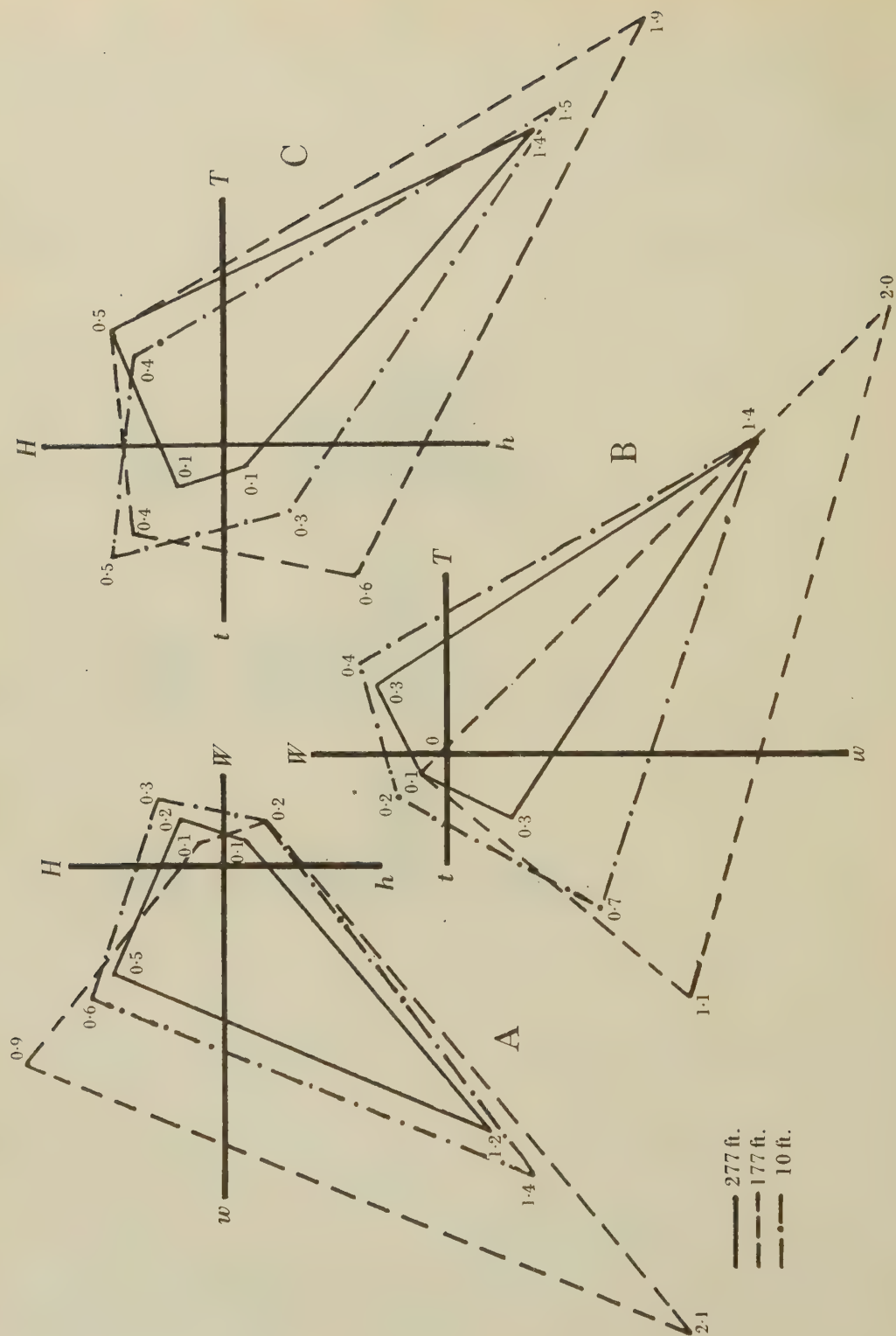
Fig. 2. The relation between density of spider population and temperature, humidity and wind velocity considered in combination.
A. Humidity and wind velocity. B. Temperature and wind velocity. C. Temperature and humidity.

taking off or alighting. The number of collections actually made in the air is small: Glick (1939) collected some 1500 spiders at heights of 200–1500 ft.

Table 7. *The average density of spider population according to the direction of the wind*

Direction	No. of observations	Average population densities		
		277 ft.	177 ft.	10 ft.
W. to N.	5	0·2	0·1	0·3
N. to E.	9	0·9	1·6	1·0
E. to S.	6	0·1	0·2	0·1
S. to W.	11	0·4	0·6	0·5

highest during June, 106 of the total being taken on three occasions. Mites were also carried on the bodies of certain insects, including the Diptera *Sciara* spp. (Sciaridae), *Leptocera* spp. (Borboridae) and *Megaselia* sp. (Phoridae). It is of interest to note that they were arranged in a symmetrical manner on the abdomen or thorax of the carrier.

The dispersal of mites by wind currents has been recorded by Stabler (1913), who showed that red spiders were carried by light south winds over a distance of 650 ft.; and by Glick (1939) who took mites at heights up to 3000 ft., both free and on the bodies of insects.
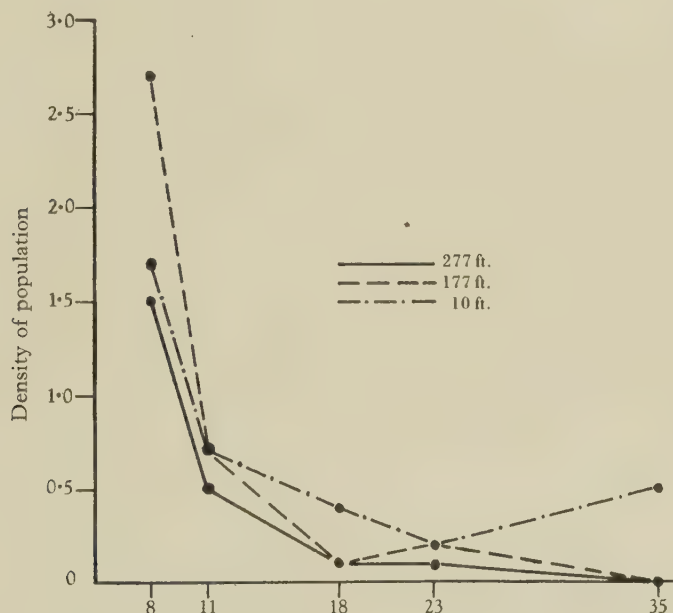

Fig. 3. The relation between wind velocity and density of spider population.

in the United States, 80 % of these being Linyphiidae. Collins & Baker (1934) captured spiders at heights of 300–2000 ft. in Massachusetts. The capture of spiders over the North Sea by Hardy & Milne (1937) has already been mentioned. Bristowe (1939–41) gives an analysis of the collections forming the basis of the present paper: the discrepancy between the total figures is due to the inclusion here of some 30 unidentified spiders.

6. A NOTE ON THE OCCURRENCE OF MITES IN THE AIR

Only 17 of the 157 unidentified mites were taken above ground-level (10 ft.): the numbers were

7. SUMMARY

The distribution of spiders in the air up to about 300 ft. was investigated by trapping in nets flown from wireless masts at Tetney, Lincolnshire, during 1934 and 1935. The spiders, of which a full list is given, showed a fairly even distribution in the air, the majority being adult and immature Linyphiidae and the young stages of other families. The largest numbers of spiders were found in the air when the temperature was in excess of 64° F., the relative humidity below 60 % and the wind velocity below 12 m.p.h., the last factor having apparently the greatest influence. The occurrence of mites, both free and on the bodies of insects, is also recorded.

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A CHESHIRE STARLING ROOST, 1944–5

By F. J. BROWN

(With 4 Figures in the Text)

1. INTRODUCTION

The winter of 1944–5 brought an exceptionally large number of starlings to roost at a fox covert, known as Groby Gorse, about a mile north of Crewe. This covert has been occupied by summer and winter flocks for at least 25 years, but it was evident in late October 1944 that some hundreds of thousands of starlings (*Sturnus vulgaris*) were assembling there in the late afternoons. In January 1945, at the beginning of a spell of severe weather, there was a noticeable increase in the number of birds using the roost and there appeared to be no decrease until the flocks broke up about 15 March. A few thousands remained until the middle of April, but afterwards the roost was completely deserted.

The covert is situated in the south-east corner of the Cheshire Plain, which is surrounded by hills 400–600 + ft. above sea-level, except on the northern side, where there is no land above 300 ft. as far as the Mersey, 20 miles distant (see map, Fig. 1). On the eastern side, 7½ miles away, the Staffordshire hills rise to 1000 ft. at one point. At their nearest points, the hills to the south and west are 10 miles distant and they are intersected by a number of gaps. The avoidance of hills by starlings on their daily flights to and from a roost has been recorded by Marples (1934); and from information received from places outside the East Cheshire Plain it is almost certain that the hills restricted the starlings' daily movements, except where the gaps provided easy access to remote feeding grounds in North Shropshire and the western portion of the Cheshire Plain.

The covert stands on ground which falls to the east, the boundary on that side being 150 ft. above sea-level, and the western margin is about 20 ft. higher. Deciduous trees constitute the perimeter of the covert, forming a dense screen on the northern side. For about 20 yd. inwards, black and 'white' thorns (*Prunus spinosa* and *Crataegus*) have been set in rows, 2 yd. apart, but they have not been 'laid' extensively. These thorns have grown to about 16 ft. and have formed a thick canopy. The inner portion has been more thickly set, and 'laid', making it most difficult to traverse, but the thorns are only about 10 ft. high. The covert is about 8 acres in area, of which the inner portion occupies about 5 acres.

It was this inner portion which the starlings used as a roost, screened from the prevailing winds, and particularly from northerly winds, by the taller thorns, the deciduous trees and the fall of the land. The configuration of the covert would appear to make it most suitable as a winter roost, and the increase in the number of birds which came to it during severe weather tends to confirm this opinion.

The thorns of the inner portion contained much dead wood, and tangled masses of broken-down branches lay here and there, but no breakage of 'green' timber was found. Damage which could be attributed to starlings, and that the accumulation of years, seemed to be due more to the harmful effects of the birds' excretions than to fracture by overcrowding.

To avoid confusion, the times given in the following records have been corrected to Greenwich mean time.

2. ASSEMBLY

The assembly of the starlings and their descent into the roost was watched on fourteen afternoons between 4 November and 10 March. The zone in which they assembled was roughly three-quarters of a circle in shape, having the covert as centre and a radius of about three-quarters of a mile. The quadrant in which no assembly took place lay between north-east and south-east, and it is significant that during dispersal and assembly very few birds were seen to pass between these two points. Thus the spread from this roost was chiefly westward, but the marked avoidance of the country lying to the east was strange. The Staffordshire hills, which would have restricted the starlings' movements if they had flown in that direction, are 7½ miles away, and their influence would not account for the birds' failure to occupy the intervening country. Very few starlings were seen during the winter near Alsager, 6 miles east-south-east of the covert, and no passage of flocks was noticed—a report which agreed with observations made at the roost.

The time when the first starlings entered the assembly zone was noted, as were also the succeeding stages of communal activity. The records of assembly are shown in Table 1 and Fig. 2. It will be noticed that assembly began at a varying interval before sunset and at a time which approached sunset as the days became shorter. On 6 January the starlings did not begin to assemble until 1 min. after

sunset. The following week assembly was complete a minute after sunset, an unusual occurrence at that time of the year, which was probably due to a complete cover of low cloud and poor visibility. In February and March, the first flocks came in at a time which was considerably earlier than sunset, the longer hours of daylight provided ample time for feeding and enabled the birds to assemble mostly before sunset.

The duration of assembly showed seasonal variation. Between 4 November and 2 December the time decreased from 38 to 24 min. The next four
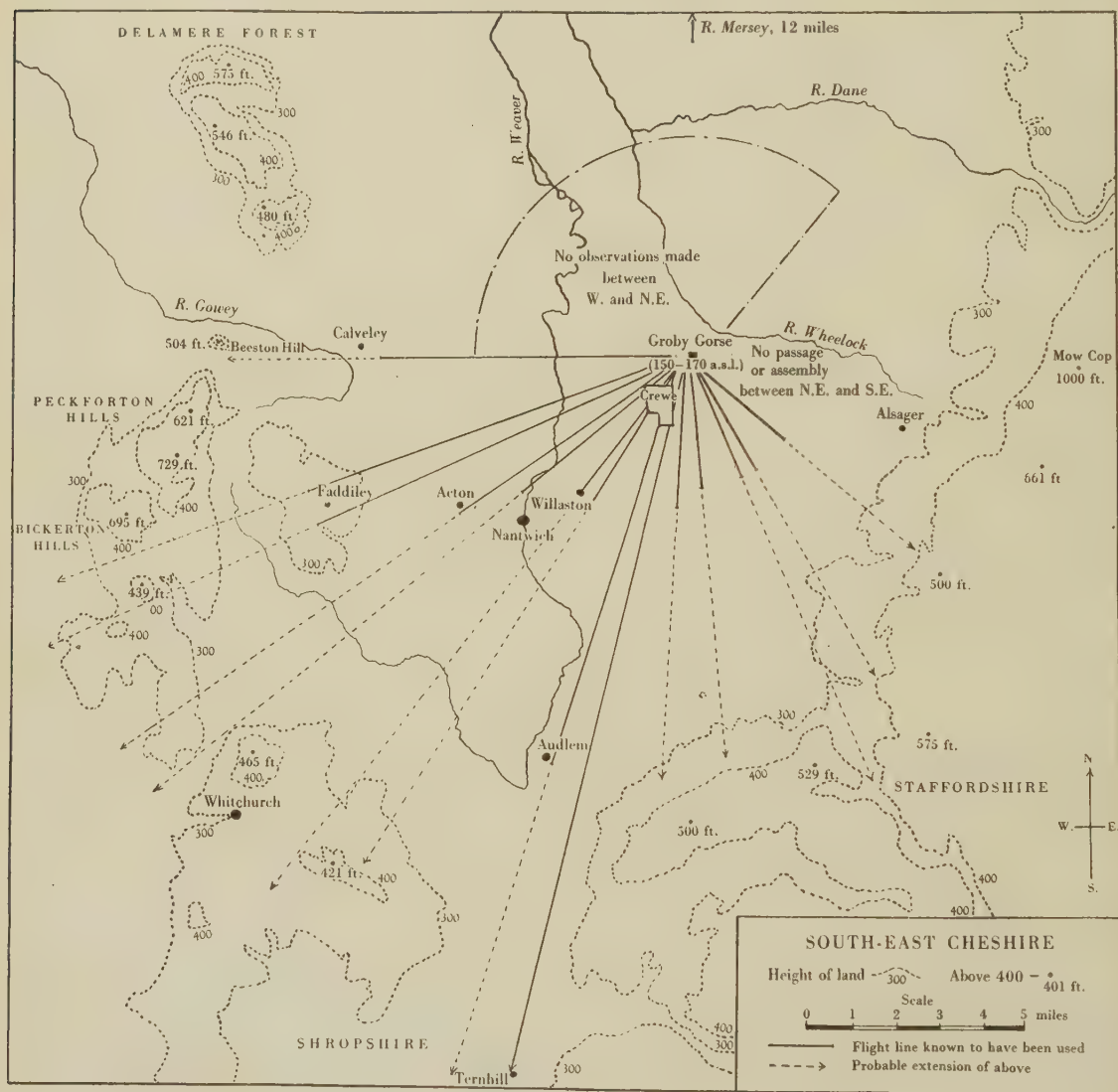

Fig. 1.

maximum being 52 min. on 24 February. It was evident that during the short hours of daylight prevailing in December and early January, the starlings remained as long as possible at their feeding grounds, with the result that assembly took place mostly after sunset, and the late arrivals returned to the roost in advanced dusk. Before and after this period, the observations showed a constant 17 min., which proved to be the minimum time. Subsequently, the time increased to a maximum of 60 min. on 3 March. It was thus obvious that when the hours of daylight were short, the time spent in assembly was curtailed, but at other periods there were sufficient hours of daylight for feeding and communal activity. Boyd

(1932), in his paper on another Cheshire starling roost, recorded 60 min. for assembly on 1 March 1930, and suggested that the duration of assembly might be found to vary at other times of the year. The records set out in Table 1 and Fig. 2 show that such was the case.

During December and January it was also apparent that considerably fewer birds were taking part in the communal activity of assembly than in November. In fact, the majority came straight to the

The time spent in communal flight also showed periodical variation, similar to the duration of assembly. It decreased in duration from November until the longer hours of daylight provided time for prolonged communal activity. The duration is shown in Table 2. The descent was made in a remarkably short time, considering the number of birds involved. The average time for all observations was 92·3 sec. The most remarkable feat was on 10 March, when a full assembly rained down in 55 sec., a much shorter

Table 1. *Beginning and completion of assembly, relative to sunset, and duration*

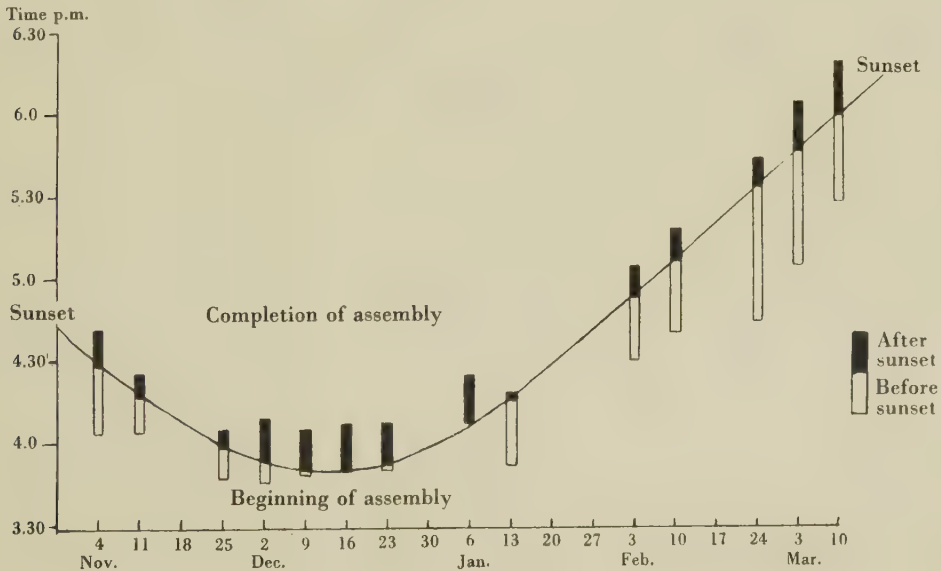|	November			December				January		February			March	
	4	11	25	2	9	16	23	6	13	3	10	24	3	10
Beginning (min.)	−26	−16	−12	− 8	− 2	Sunset	− 2	+ 1	−24	−25	−28	−52	−44	−34
Completion (min.)	+12	+ 6	+ 6	+16	+15	+17	+15	+18	+ 1	+10	+10	+ 7	+16	+18
Duration (min.)	38	22	18	24	17	17	17	17	25	35	38	59	60	52

− = before sunset; + = after sunset.

Fig. 2. Assembly.

roost and went down without any preliminary activity within the assembly zone. On 23 December the number of birds which assembled and took part in communal flight and the descent was only about 20,000, a small fraction of the total number. They went down at 3.55 p.m., but vast numbers continued to come in for 12 min. and to drop immediately into the roost. At that time of the year, assembly was not only curtailed, as previously stated, but was dispensed with altogether by most of the starlings. Virtually all the flocks took part in the communal activities at other periods.

time than was required for some of the partial assemblies to come down. The maximum time was recorded a week earlier, when the attacks of seven kestrels prolonged the descent to 190 sec.

Unless weather conditions were adverse, it was noticed that the starlings came into the assembly zone at two distinctly different heights. Some came in at about 50–100 ft., but others flew in at about 150–200 or more ft., and though some of the early arrivals came in at the greater height, a much greater number did so towards the end of assembly. A similar variation was to be seen at Willaston, 4 miles south-west

of the roost, on one of the flight lines. There, flocks of 4000–5000 birds often passed over on their way to the roost at about 200 ft., and it was evident that a preliminary assembly had been made some distance away. Birds feeding in the Willaston district rose to about 50 ft. when they left for the roost and continued to fly at that height, as far as they could be seen with glasses. Thus, it is probable that the high-flying starlings were those which had come from the distant feeding grounds, and it was these birds which arrived at the roost towards the end of assembly.

intervals. On most mornings, at some time before sunrise, a few hundred starlings rose for a momentary flight, usually within the bounds of the covert, and settled again. Soon afterwards the first departure took place and other flocks left at irregular intervals. On one occasion there were five departures: once they left in three immense flocks, and on four mornings there were four departures. Fig. 3 shows the time of departure of the first and last flocks relative to sunrise. It shows that from 25 November to 3 February dispersal was completed,

Table 2. *Duration of communal flight*

November			December				January		February			March	
4	11	25	2	9	16	23	6	13	3	10	24	3	10
Duration (min.) 19	12	7	10	8	5	2	3	11	3	4	18	22	32

Table 3. *Beginning and completion of dispersal, relative to sunrise and duration*

	25 Nov.	23 Dec.	20 Jan.	3 Feb.	3 Mar.	10 Mar.
Beginning (min.)	−17	−2	−12	−19	−8	−10
Completion (min.)	−1	+12	+11	+7	+19	+21
Duration (min.)	16	14	23	26	27	31

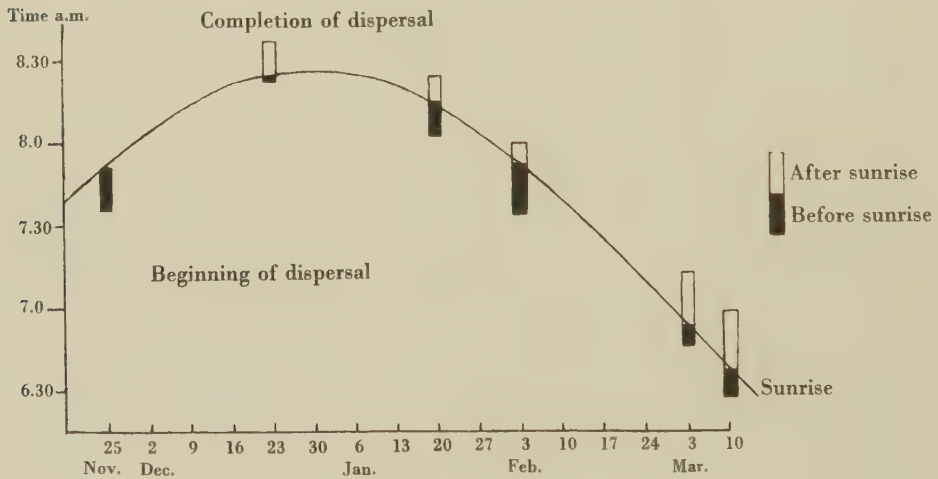− = before sunrise;   + = after sunrise.

Fig. 3. Dispersal.

Boyd stated that the first birds to leave in a morning were those which had the longest flight to make, and, as just stated, it is probable they were among the last to return. By their early departure and late return, they would spend little less time at their feeding grounds than those which fed nearer to the roost.

3. DISPERSAL

Dispersal was watched at least once each month, but the observations could not be made at regular

or the greater part was effected, before sunrise, with the exception of 23 December, when it was undoubtedly delayed by fog. At this period of the year the starlings left the roost as soon as daylight and weather conditions permitted. In March the greater part of dispersal took place after sunrise, and it would appear that with longer hours of daylight the necessity of an early departure was less urgent. The duration of dispersal showed seasonal variation, similar to the duration of assembly (Fig. 1). It decreased from 16 min. on 25 November to 14 min. on

23 December, but afterwards it increased to a maximum of 31 min. on 10 March. Boyd recorded 60 min. for dispersal on 1 March, the same time as for assembly, but at this roost such similarity of time for assembly and dispersal was not found. When both were observed on the same day, assembly required the longer time, the excess being:

25 Nov.	23 Dec.	3 Feb.	3 Mar.	10 Mar.
2 min.	3 min.	9 min.	33 min.	21 min.

Observations at Willaston in November showed that there was considerable variation in the number of birds using that flight-line, and this fact suggested the possibility that the recording of the direction taken by the greatest numbers during dispersal might

The change in direction lay between north and south-west, and it is noteworthy that it was between these two points of the compass that the physical features of the plain allowed the greatest freedom of movement. It would appear that all the starlings do not visit the same localities throughout the winter; some may do so, but others appear to be more nomadic and change their feeding grounds from time to time. Wynne-Edwards (1929) found some evidence of the return of the same birds to the same place, but Boyd, as a result of ringing, found that the proportion of recaptured birds was lower than in other species. The change of feeding ground by some of the flocks would account for his failure to recover more than a few of the hundreds ringed.

Showing direction taken by greatest numbers

4 Nov.   25 Nov.   16 Dec.

23 Dec.   13 Jan.   3 Feb.

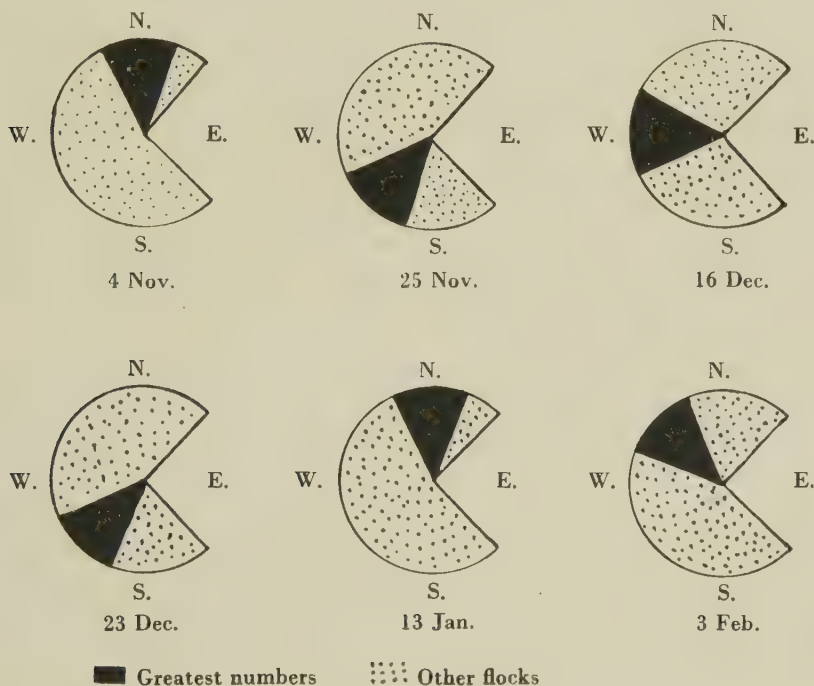■ Greatest numbers   ⋮⋮⋮ Other flocks

Fig. 4.

be worth while. It was also intended to make similar observations during assembly, but except for a few occasions it was found that the movement of flocks from one part of the assembly zone to another made it impossible to determine from which direction the greatest numbers had approached the roost. When no such movements occurred, the preponderance of numbers coming from any direction was noted, and the records are included with those of dispersal.

It was found that the direction taken by the greatest numbers changed from time to time, and the variation is shown in Fig. 4.

4. FLIGHT-LINES

In addition to the observations at Willaston, casual observations made in the Crewe district determined a number of flight-lines used by the starlings. By the time the flocks had passed over Crewe, they had separated into well-defined flight-lines. Their direction and passage over buildings and landmarks was remarkably constant, except when strong side winds caused a change of direction towards the source of the wind and the line of flight was to the windward of normal.

The map shows that between south-east and west of the roost, there were, at least, fourteen flight-lines radiating from the covert. They are shown by a continuous line as far as they were known to be used, and the probable continuation of others is shown by a dotted line. There were, of course, others passing between west and north-east, but it was impossible to observe those. The use of one line passing through a gap south-south-west of the roost was verified from Ternhill, $17\frac{1}{2}$ miles away, the greatest distance which the birds were known to have flown.

The observations at Willaston were made on sixty-two afternoons, but the records of the time of the passage of first and last flocks are so similar to those shown in Fig. 1 that their inclusion is not necessary.

Perhaps the most interesting aspect of the Willaston observations was the formation of flocks in the late afternoons, before their departure for the assembly zone. There were three periods when preliminary assembly took place, twice in two fields set with wheat, and once in a field set with oats, the periods being 25–27 November, 1–8 December and

same. The early arrivals appeared to be disinclined to come down to feed and their flight, to and fro, across the flight-line seemed to be made for the purpose of making contact with other flocks. When this had been achieved, they came down to feed and were usually joined by others. Such preliminary assemblies were observed in four other localities, at one point 6 miles from the roost, and it was obvious from the size of some of the flocks passing over Willaston, that assembly had taken place some miles farther away. From these observations it would appear that assembly was a complex procedure, by no means confined to the assembly zone, for it often took place miles away from the roost. The places where preliminary assembly took place were changed from time to time, and those fields known to be used were those which had been recently ploughed or set with wheat or oats.

The variation in the number of starlings using the Willaston flight-line early in November has been mentioned, and a note was made, at each observation throughout the winter, of the approximate number of birds passing over on their way to the roost. The

Table 4. *Weekly average number of starlings using the Willaston flight-line (approx.)*

	November				December					January				February				March	
	4	11	18	25	2	9	16	23	30	6	13	20	27	3	10	17	24	3	10
No. (in 1000's)	3	1	1	3	8	7	1	4	2	1	3	1	1	2	4	2	2	1	1

8–23 February. As the behaviour of the birds was essentially the same on all occasions, the observations on 1 December (when the fullest notes were made) may be taken as typical.

On that day, at 3.10 p.m., about fifty starlings appeared from the west and passed over the wheat field eastwards. After a few minutes they returned, and flying over the field, turned northwards and settled in a poplar tree 300 yd. away. Shortly afterwards about 100 came from the south, and after turning eastwards they returned and were joined by the first arrivals. The combined flock continued to fly east and west, passing over the wheat field each time. At 3.20, about 1000 came from the west, and the two flocks having joined together, they flew in a north-westerly direction for about 400 yd., where they met another flock of about 1000, which had come from the south-west. The whole flock then flew straight to the wheat field and began to feed. Other flocks from the south-east, south and south-west came down and eventually there were about 5000 birds present. They left for the assembly zone at 3.47, in a north-north-east direction.

The number of birds taking part in these preliminary assemblies varied, from time to time, from about 2000 to 10,000, but the procedure was the

weekly average of these numbers is shown in Table 4. The least number of birds using the flight-line was about 1000, usually in several flocks, but at irregular intervals there was a considerable increase, due to the passage of large flocks which had assembled miles away, and to the preliminary assembly of flocks near to Willaston. Fig. 4 shows that though some of the starlings may have returned to the same localities daily, others only used the flight-line for a short period and so changed their feeding grounds from time to time. These observations are complementary to those made at the roost concerned with the direction taken by the greatest numbers and Fig. 4 shows that when the greatest numbers left the roost in a south-west direction, on 25 November and 23 December, there were decided increases in the number of birds using the Willaston flight-line.

5. BIRD AND ANIMAL ASSOCIATIONS

As the starlings occupied only the inner portion of the covert, the remaining 3 acres were available for use by other species and visits made in the early mornings showed that a number of species roosted there. Two herons (*Ardea cinerea*) were seen in a chestnut tree at dawn on 25 November, and they, or

others, were found there until the end of January. Their presence was due to a 'flash' (a mere caused by subsidence due to brine-pumping), a few hundred yards away. Jays (*Garrulus glandarius*) and magpies (*Pica pica*) were seen or heard in the covert on most visits, before dispersal and after assembly. Magpies were the more numerous and at 4 p.m. on 3 February, twelve were engaged in communal display on the western side of the wood. A week later fifteen were found in an adjoining field and later they flew into the trees on the northern side. Rooks (*Corvus frugilegus*) did not use the covert, but small parties of jackdaws (*C. monedula*) did so. A number of carrion crows (*C. corone*) roosted there and frequented the adjoining fields, where they were often seen feeding on dead starlings.

A score of fieldfares (*Turdus pilaris*) left the covert before dispersal on 20 January, the only occasion they were known to have roosted there, although numbers frequented the locality. Other passerines which used the covert included the blackbird (*T. merula*), robin (*Erithacus rubecula*), hedge sparrow (*Prunella modularis*), wren (*Troglodytes troglodytes*), chaffinch (*Fringilla coelebs*), great tit (*Parus major*) and blue tit (*P. caeruleus*).

One sparrow hawk (*Accipiter nisus*) was known to roost in the covert, for it was often seen to leave before or during dispersal. On 23 December it left the covert 32 min. before dispersal began (a late departure due to fog), and after beating the nearby hedgerows, it continued to fly in and out of the covert until all the starlings had gone. From December to the middle of February, two kestrels (*Falco tinnunculus*) were to be found in the afternoons circling over the locality awaiting the incoming starlings. Two were present as usual on 24 February, but four others accompanied the assembling flocks and harassed them for ten minutes. A week later seven kestrels were present and they continued to attack the flocks for half an hour. They were not known to roost there.

Apart from the attacks by predatory species, there was no evidence of any hostility between the starlings and the other birds occupying the roost. This was probably due to the fact that the starlings occupied only the inner part of the covert, thus leaving the remainder available for other birds if they chose to use it.

The only evidence of the presence of a fox (*Vulpes vulpes*) was found on 20 January, when snow lay on the ground. Its footmarks showed where it had left, and returned to, the covert. The absence of rabbits (*Oryctolagus cuniculus*) was almost certainly due to their extermination during the war, and not a disinclination on their part to use the covert.

6. ACKNOWLEDGEMENT

In conclusion, I express my sincere thanks to Major A. W. Boyd for his valuable suggestions and advice, so readily given, while the observations were being made, and in the preparation of this paper.

7. SUMMARY

1. The times of dispersal and assembly relative to sunrise and sunset respectively, of a roost of starlings (*Sturnus vulgaris*), near Crewe, showed seasonal variation.

2. The duration of communal flight and assembly also varied with the time of the year, both being curtailed or dispensed with, during midwinter.

3. Definite flight-lines were regularly used, but the number of birds using one line varied considerably, showing that some of them changed their feeding ground from time to time.

4. Preliminary assembly often took place at remote points. Birds going to distant feeding grounds dispersed first and returned late during assembly, thus spending little less time at their feeding grounds than those not going so far.

5. Starlings occupied one part of the wood and other species of birds used the remainder without any sign of hostility.

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A SURVEY OF THE DISTRIBUTION OF THE AMERICAN GREY SQUIRREL (*SCIURUS CAROLINENSIS*) AND THE BRITISH RED SQUIRREL (*S. VULGARIS LEUCOURUS*) IN ENGLAND AND WALES IN 1944–5

By MONICA SHORTEN, *Bureau of Animal Population, Oxford University*

(With 5 Maps in the Text)

1. INTRODUCTION AND ACKNOWLEDGEMENTS

The introduction and spread of the American grey squirrel (*Sciurus carolinensis* Gmelin) in the British Isles, has been described by Middleton (1930, 1932, 1935) and Parsons & Middleton (1937); but since the last survey by these authors in 1937 no large-scale investigation into the distribution of the grey squirrel has been made. Little was known of the precise areas inhabited by the native red squirrel (*S. vulgaris leucourus* Kerr); thus the effect of the introduced squirrel on the distribution of our native species was also not known with any accuracy.

The present paper describes the results of a survey carried out between August 1944 and December 1945, which had as its object the collecting of data from every parish in England and Wales on the presence or absence of the grey and the red squirrel.

The author's warmest thanks are due to Mr C. Elton and Mr A. D. Middleton, who gave much assistance in planning the survey; and to officials of the War Agricultural Executive Committees in the counties of England and Wales who did most of the distribution and collecting of the forms: indeed it is doubtful whether the survey could have been carried out with any degree of completeness without their help. Thanks are also due to the Forestry Commission, who collected data from their foresters in Scotland, Devon, and Yorkshire. Members of the Lincolnshire Naturalist's Union and the Lancashire and Cheshire Fauna Committee supplied valuable information, and park superintendents in the big towns and cities also gave help. Among the numerous individual helpers I should like to thank Mr F. T. Baker, Major A. W. Boyd, and Mr R. S. R. Fitter for the help they gave in difficult areas.

This investigation was carried out with the aid of a grant from the Agricultural Research Council.

2. METHODS

In most of the counties of England and Wales information was gathered through the War Agricultural Executive Committees, either directly from their parish representatives, or through district officers, who collected the data and filled in the forms. The questionnaires were made as simple as possible, the observers being asked to strike out 'yes' or 'no' opposite 'Grey squirrels present' and 'Red squirrels present'; and to fill in the name of the county and parish for which they were replying. In most cases the forms were returned to the local committee, and forwarded to Oxford for analysis in bulk. In some borderline areas, where the grey squirrel is rare, replies were checked to ensure that there had not been confusion between the two species. The grey squirrel has a certain proportion of reddish brown in the summer coat, and the red squirrel becomes partially bleached, especially about the tail, from March to September. It is possible that in a few cases this confusion may have led to false reports.

A map of each county in England and Wales (scale $\frac{1}{2}$ in. to 1 mile) with the parish boundaries marked, was filled in with the data from the forms. A sheet of tracing paper, with the 10 km. (National) grid ruled on it was placed over the completed map, and the results transferred to a small-scale map marked with the same grid. Squares in which parishes having red or grey squirrels were included were marked with a symbol indicating this. Where a parish overlapped the line of the grid, its data were referred to that square where the major part of the parish lay; or, in some cases, where the wooded part lay, if this was not in both the squares. Where no squirrels were reported to be in all the parishes lying in a square, it was marked with a negative symbol. Squares where most parishes reported no squirrels, but some were still not covered, were left with a query mark.

The Forestry Commission areas in Scotland were sent a rather more detailed form, asking about numbers and fluctuations, as well as presence and absence. This applied mainly to the red squirrel. The areas of each forest from which information had come were filled in roughly on the small-scale map, and the squares largely occupied by the forest were filled in with the appropriate symbol. No complete picture of the status of the red squirrel in Scotland

could be expected by this method, but a picture of the position in the Commission areas was gained.

The London area was covered by replies from the superintendents of the various parks and open spaces to a form asking for 'presence or absence' data, and for any known facts about the past history of the two species in each place. The same type of questionnaire was sent to parks in the big towns and cities all over the country.

When these replies had been mapped, areas that were still incompletely covered were dealt with through correspondence, press appeals, and the help of local naturalists' societies.

Any suspicious reports were checked, where possible, through an independent observer. Where corroboration was lacking, the record was counted as valid if the observer repeated his statement on inquiry. A mass of data from other sources (private correspondence from naturalists, observers who helped with the 1937 survey, and other interested people; press cuttings from numerous papers and magazines; personal communications, etc.) tallied in a most encouraging way with the information collected in the parish survey. All the records from this and previous inquiries are filed in the Bureau of Animal Population.

3. RESULTS

Table 1 summarizes the results of the parish survey numerically, while Maps 1a and 1b show them diagrammatically. Maps 2a, 2b and 2c, based on the parishes covered in each county, give the percentages of parishes with grey, red, and 'no squirrels'.

In Table 1 the extent of the survey can be gauged by reference to column 3 where the percentage of parishes covered in each county is given. 77% of the total number of parishes in the whole of England and Wales were covered. The response was poor in two counties only: Northumberland and Devon. From columns 5 and 7 the percentage of covered parishes having grey and red squirrels respectively

The results of the Forestry Commission inquiry in Scotland can be summarized here. The total number of forests which supplied information was 120. Of these, four reported the grey squirrel; 92 reported the red squirrel (77%), 16 of these stating 'Few, if any'; 24 forests reported having no squirrels (20%); three had both red and grey, and one grey only. The four forests reporting the grey squirrel were Tulliallan in Fife; Garadhban in Stirlingshire, Devilla in Fife, and Twiglees in Selkirkshire. The last named reported the grey squirrel only, and the accuracy of the report is rather doubtful, as no grey squirrels have previously been reported anywhere in that area.

The foresters were asked to state whether the red squirrel had increased or decreased during the past five years, and whether it was at present rare, common, or numerous.

Of the 92 forests reporting red squirrels:

    16 reported few if any,*
    68 reported few,
    8 reported numerous.

Of forests reporting few red squirrels:

    13 reported an increase,
    32 reported no change,
    23 reported a decrease.

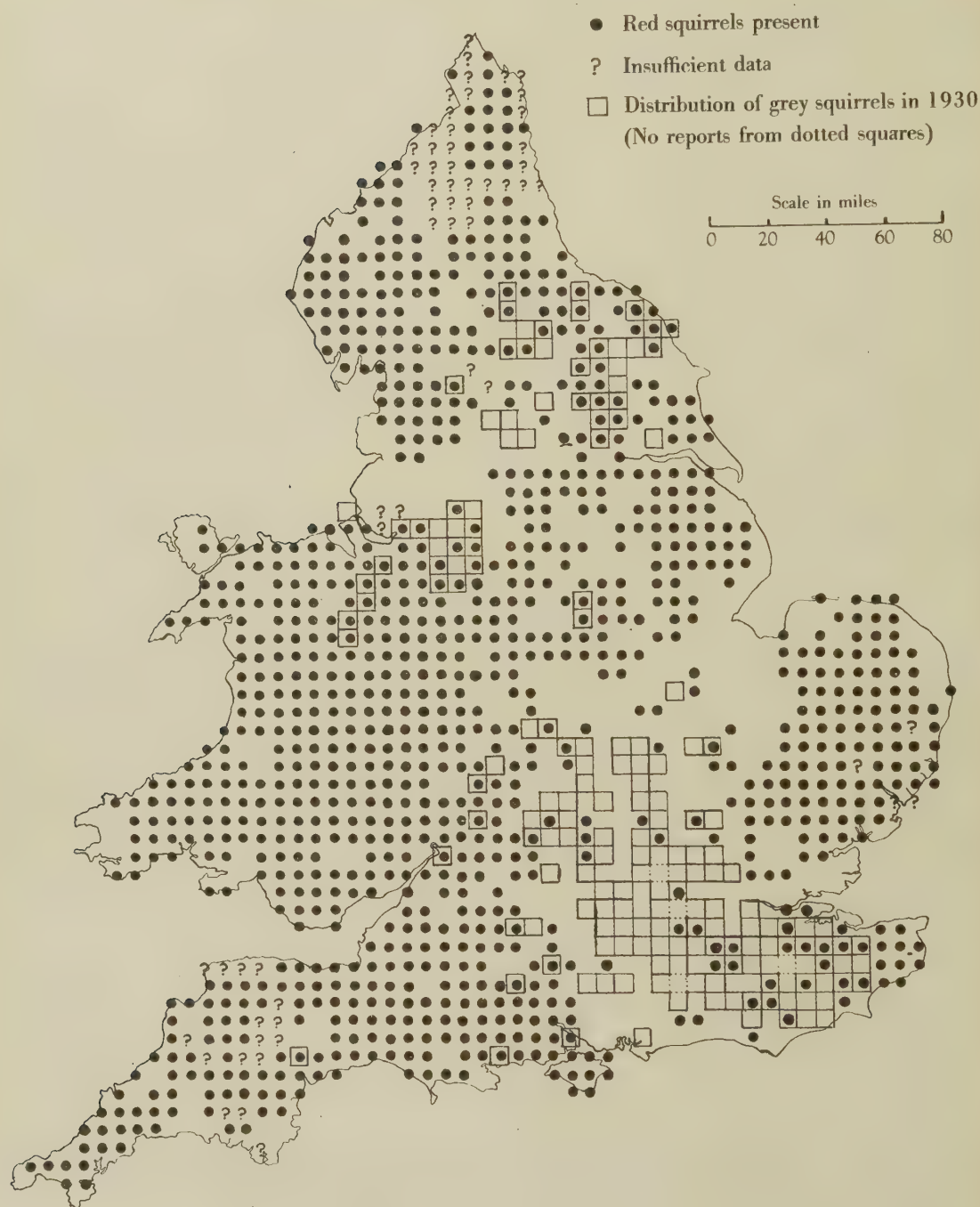Of forests reporting numerous red squirrels:

    3 reported an increase,
    3 reported no change,
    2 reported a decrease.

Totals: Increase, 16. No change, 35. Decrease, 25.

Grey squirrels were reported by the foresters in Scotland at Luss (Dumbartonshire); on the east side of Loch Fyne (Argyllshire); in West Fife; at the Falls of Leny, Callander, Doune, near Gartmore, and in the Earn Valley at Comrie (all in Perthshire); and at the Carse of Stirling. They were also reported to be found on the Linlithgow estate near Edinburgh.

The City Parks inquiry brought in fifteen replies, which are summarized below:

Grey squirrels present	Red squirrels present	Both species present	Neither species present	No reply	Uncertain
Darlington	Southampton	Bristol	Halifax	Leicester	Bradford
Exeter	Liverpool	Birmingham	Salisbury	—	—
Nottingham	Derby	—	—	—	—
Leeds	Sheffield	—	—	—	—
Manchester	Stafford	—	—	—	—

can be seen; a suggestion of how widespread each species is in any given county is given. Column 10 gives the percentage of parishes among those replying that were reported to have no squirrels. Squirrel-free territory was found to consist on the whole of unsuitable land, either marshy and sparsely timbered, industrialized; or in some cases, suitable, but made inaccessible by some natural barrier.

* The sixteen forests reporting 'few, if any' red squirrels, stated that this was not due to any policy of extermination, and it was suggested that illness was the main cause of the drop in numbers. Nine forests reported the decrease in numbers of the red squirrel to be due to the felling of trees in the period under consideration. At Garadhban the decrease was attributed to the increase in numbers there of the grey squirrel.

● Red squirrels present

? Insufficient data

☐ Distribution of grey squirrels in 1930
(No reports from dotted squares)

Scale in miles

0   20   40   60   80

Map *1a*. The distribution of the red squirrel (*Sciurus vulgaris leucourus*) in England and Wales; showing the area occupied by the grey squirrel in 1930. 66 % of this area is now devoid of red squirrels. Period covered by survey: August 1944 to December 1945.

• Red squirrels present

? Insufficient data

☐ Distribution of grey squirrels in 1930

(No reports from dotted squares)

Scale in miles

0 20 40 60 80

Map 16. The distribution of the grey squirrel (*Sciurus carolinensis*) in England and Wales. County boundaries and the 10-kilometre (National) grid shown. Period covered by survey: August 1944 to December 1945. The distribution of red and grey squirrels alone and both together is seen from laying Map 15 over Map 16. The contrast is best when the maps are held up against the light.

● Red squirrels present

? Insufficient data

☐ Distribution of grey squirrels in 1930
(No reports from dotted squares)
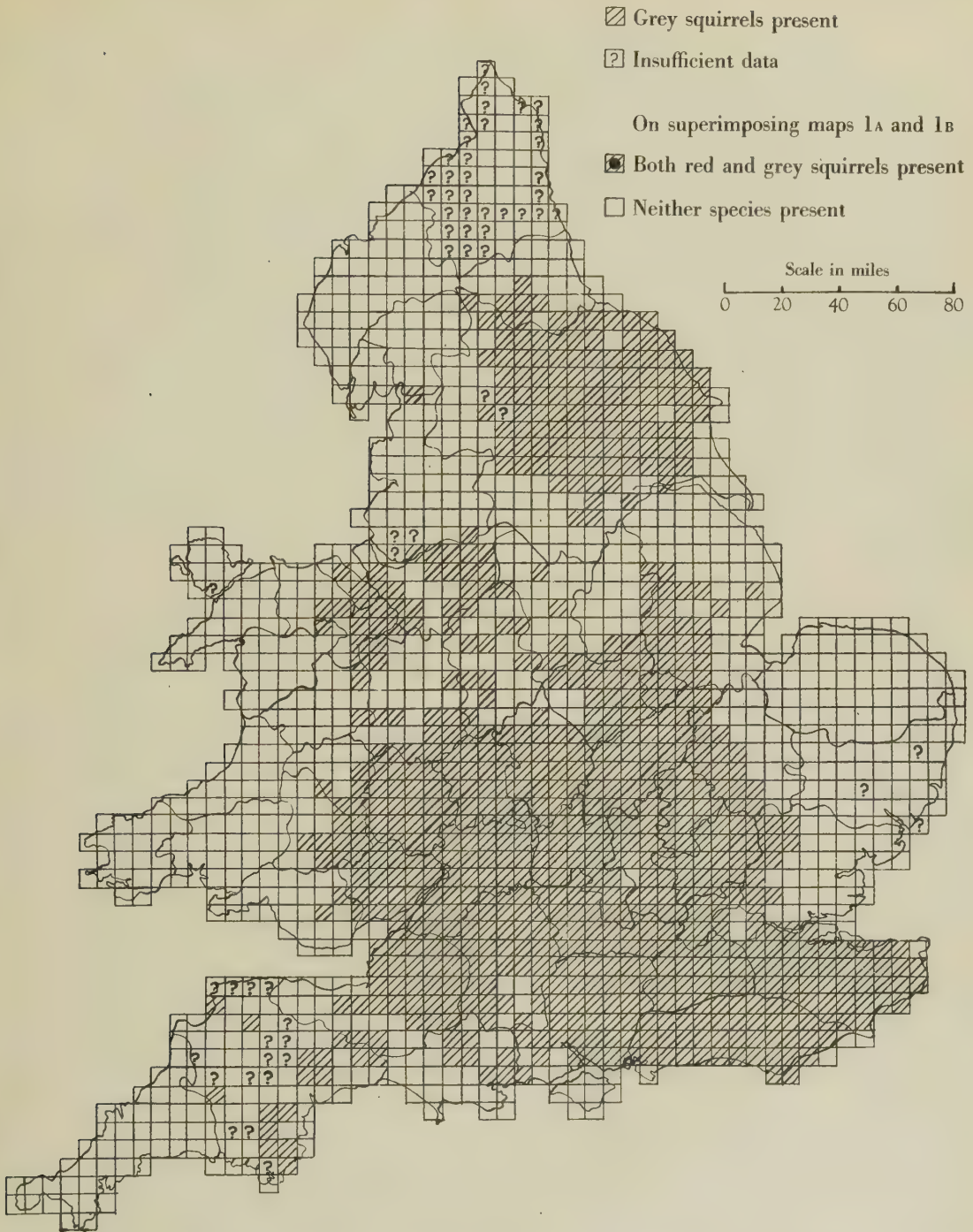
Scale in miles

0   20   40   60   80

Map 1 a. The distribution of the red squirrel (*Sciurus vulgaris leucourus*) in England and Wales, showing the area occupied by the grey squirrel in 1930. 66 % of this area is now devoid of red squirrels. Period covered by survey: August 1944 to December 1945.

☑ Grey squirrels present

? Insufficient data

On superimposing maps 1A and 1B

◼ Both red and grey squirrels present

☐ Neither species present

Scale in miles
0   20   40   60   80

Map 1b. The distribution of the grey squirrel (*Sciurus carolinensis*) in England and Wales. County boundaries and the 10-kilometre (National) grid shown. Period covered by survey: August 1944 to December 1945. The distribution of red and grey squirrels alone and both together is seen from laying Map 1a over Map 1b. The contrast is best when the maps are held at arm's length.

Table 1. *Results of the parish survey*

Columns 5 and 7 are drawn from the figures in columns 4 and 6, plus column 8 in each case.

| | Parishes in county | | | | | | | | |
County	Total in county (1)	No. covered (2)	% covered (3)	No. with grey squirrel (4)	% with grey squirrel* (5)	No. with red squirrel (6)	% with red squirrel* (7)	No. with both species (8)	No. with neither (9)	% with neither* (10)
Anglesey	62	11	18	0	0	6	55	0	5	45
Bedfordshire	124	106	86	106	100	0	0	0	0	0
Berkshire	185	185	100	167	90	0	0	0	18	10
Brecknockshire	89	89	100	0	37	56	100	33	0	0
Buckinghamshire	212	209	99	130	65	2	63	5	72	34
Caernarvonshire	53	53	100	0	0	23	47	0	30	52
Cambridgeshire	127	102	80	21	25	17	21	4	60	59
Carmarthenshire	70	59	84	0	0	50	85	0	9	15
Cardiganshire	78	73	94	0	0	47	64	0	26	36
Cheshire	377	282	75	47	23	56	26	18	161	57
Cornwall	195	195	100	0	0	86	44	0	109	56
Cumberland	153	149	98	0	0	70	47	0	79	53
Denbighshire	81	41	51	4	27	24	76	7	6	15
Derbyshire	289	266	92	3	3	30	13	4	229	86
Devonshire	448	153	34	14	79	76	55	8	55	36
Dorsetshire	267	242	90	1	5	140	62	10	91	38
Durham	196	196	100	2	3	52	29	4	138	10
Essex	332	303	91	16	20	83	42	43	161	53
Flintshire	49	48	98	15	40	18	46	4	11	23
Glamorganshire	141	106	75	2	3	51	49	1	52	49
Gloucestershire	306	216	69	126	85	9	31	57	24	11
Hampshire	256	254	99	152	77	24	27	44	34	13
Herefordshire	250	128	51	27	81	25	79	76	0	0
Hertfordshire	546	339	70	146	59	93	46	64	36	11
Huntingdonshire	89	88	99	59	76	0	9	8	21	24
Isle of Ely	32	32	100	0	0	0	0	0	32	100
Isle of Wight	20	20	100	0	0	17	85	?1	2	10
Kent	336	334	100	198	78	4	20	62	70	21
Lancashire	353	310	88	0	1	78	26	2	230	74
Leicestershire	228	227	100	107	56	4	11	21	95	42
Lincolnshire: Holland	44	44	100	1	2	0	0	0	43	98
Kesteven	161	118	73	50	61	7	25	22	39	33
Lindsey	424	103	24	1	3	61	61	2	39	38
Monmouthshire	83	83	95	4	63	13	74	48	18	22
Montgomeryshire	62	62	100	0	3	60	100	2	0	0
Merionethshire	39	39	100	0	1	37	95	0	2	5
Middlesex	32	30	94	27	94	0	0	1	2	6
Nottinghamshire	243	240	99	1	3	47	22	5	187	78
Norfolk	539	380	71	0	0	102	27	0	278	73
Northamptonshire	270	261	97	206	81	2	3	5	48	18
Northumberland	468	76	16	0	0	61	80	0	15	20
Oxfordshire	237	172	73	144	90	1	6	10	17	10
Pembrokeshire	164	164	100	0	0	54	67	0	110	33
Peterborough (Soke of)	26	25	96	13	72	0	20	5	7	28
Radnorshire	63	26	41	1	19	21	96	4	0	0
Rutlandshire	58	58	100	58	100	0	0	0	0	0
Shropshire	251	227	91	1	15	154	82	33	39	17
Somersetshire	416	358	89	53	44	107	59	110	88	24
Staffordshire	217	153	71	3	13	62	52	17	71	47
Surrey	131	107	82	88	94	0	11	12	7	7

Table 1 (continued)

County	Total in county (1)	No. covered (2)	% covered (3)	No. with grey squirrel (4)	% with grey squirrel* (5)	No. with red squirrel (6)	% with red squirrel* (7)	No. with both species (8)	No. with neither (9)	% with neither* (10)
Suffolk: East	318	137	43	0	0	69	50	0	68	50
West	173	127	73	0	0	84	66	0	43	34
Sussex	284	245	86	211	91	0	4	11	23	9
Warwickshire	244	89	37	51	62	4	17	11	23	26
Westmoreland	110	106	97	0	0	74	70	0	32	30
Wiltshire	277	270	98	89	55	35	35	58	88	33
Worcestershire	215	202	94	90	75	4	32	61	47	23
Yorkshire: N. Riding	535	510	95	213	55	26	18	67	204	40
E. Riding	206	166	81	44	40	21	26	22	79	48
W. Riding	546	387	71	103	79	69	70	200	15	4
Totals	12780	9781		2795		2316		1182	3482	
% of covered parishes			77		29		24	11		36

* Denotes percentage of total number of parishes covered, not of the total number in the county. The bottom row of percentages is calculated from the grand totals.

Table 2. *London area: Parks and Commons, other open spaces*

Locality	Grey	Red	Remarks
Royal Parks:			
Hyde Park	No	No?	
Green Park	No	No?	
St James's Park	No	No?	
Regent's Park	No	No?	
Greenwich	No	No	Grey squirrels in 1943; none since
L.C.C. Parks:			
Peckham Rye	No	No	
Battersea	No	No	
Finsbury	No	No	
Southwark	No	No	Built-up area
Victoria	No	No	
Clissold	No	No	
Dulwich	No	No	
Eltham	Yes	No	
Brockwell	No	No	
Commons, etc.:			
Clapham Common	No	No	
Putney Heath	Yes	No	Shot two a day; used to get twelve a day
Beckenham Place	Yes	No	
Hampstead Heath	Yes	No	Grey squirrel decreased in numbers
Tooting Common	No	No	
Wandsworth Common	No	No	
Streatham Common	No	No	One red squirrel in 1932
Kensington Gardens	No	No?	
Buckingham Palace Gardens	No	No?	
Shooters Hill	Yes	No	
Abbey Wood	No	No	Red squirrels here 20 years ago
Bostall Woods	No	No	Red squirrels here 20 years ago
Oxleas Wood	Yes	No	
Kenwood	Yes	No	

Note. Query mark denotes no definite answer to this; almost certainly no.

Three of these parks (Birmingham, Darlington, and Exeter) stated that the grey squirrel had been introduced there wittingly. It was stated that in Birmingham the red and the grey squirrel lived near to each other, and that there was some fighting between them. In Blaise Castle Woods, just outside Bristol, the two species were described as not living near to each other, but fighting.

from the London area, and the grey from Regent's Park.

4. DISCUSSION

(a) *The grey squirrel*

Since the last survey of its distribution (Parsons & Middleton, 1937) the grey squirrel has extended its range in England and Wales, noticeably in the west.

Map 2 *a*: The percentage of covered parishes in each county reporting the presence of the grey squirrel.

After a consultation with Mr R. S. R. Fitter a circular letter was sent to the superintendents of all the parks, and to head-keepers of commons and other open spaces, in the London area. From Table 2 it will be seen that the red squirrel has disappeared

Although the 1937 survey was not a complete one, some idea of the spread of the species can be gained from the fact that when the 10 km. grid was applied to a map of the known distribution in 1937, 274 squares contained records of the grey squirrel; the

number of squares positive for the species in 1944-5 is 708—an increase of 434 squares. 112 of these were added on to the western boundary of the territory. It must be emphasized, however, that these figures can give no true idea of the actual increase in territory, as not only were the extent and method of

the eastern boundary (running approximately along a line south-east from Kingston-on-Hull in the East Riding to Saffron Walden in Essex, then due south to the border of Kent; here the territory goes farther east to the coast). This boundary is very much the same as it was in 1937. Mapping of woodland types
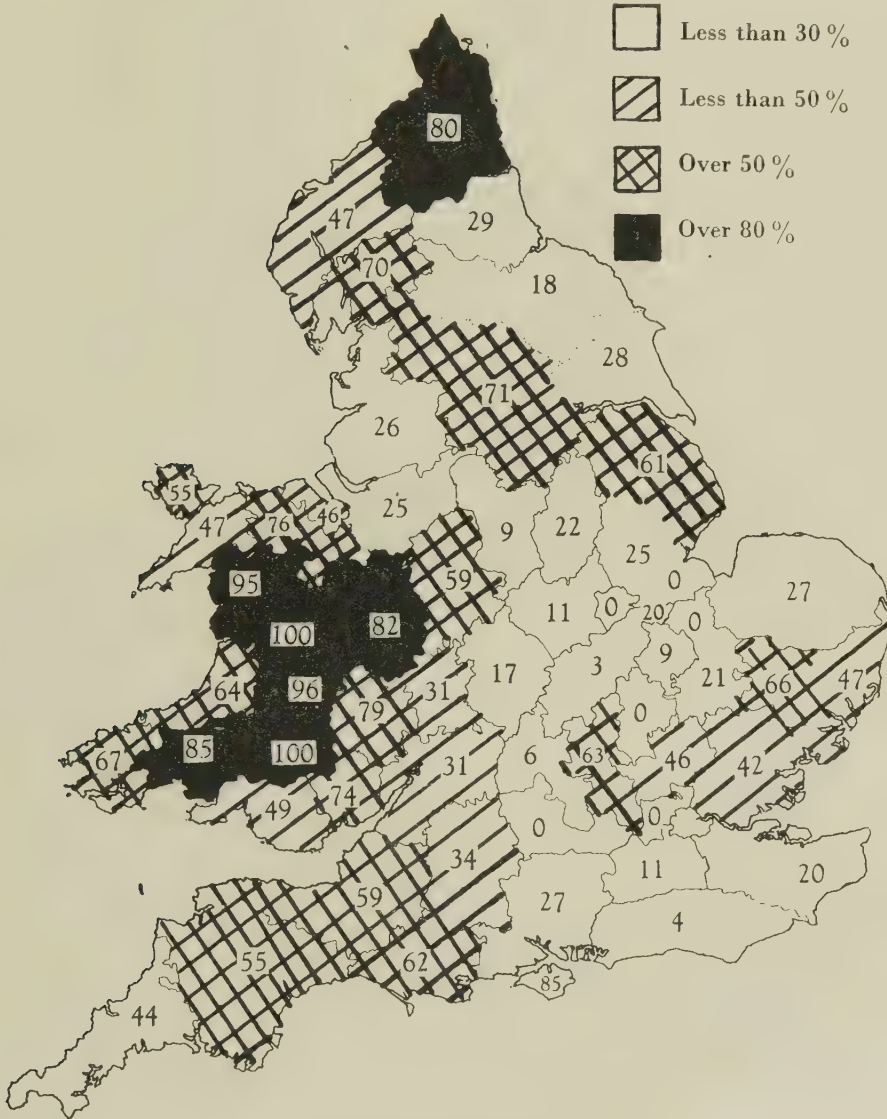
Map 2*b*. The percentage of covered parishes in each county reporting the presence of the red squirrel.

collection of data different in the two surveys, rendering comparison difficult, but the grid system over-simplifies the range considerably.

Several attempts were made to discover any factor that was influencing the distribution, encouraging the westward spread, and inhibiting any move beyond

(coniferous and deciduous) was impracticable with the grid system; both types occurred in the majority of the squares. Up-to-date information on the timber distribution proved impossible to collect. No satisfactory explanation of the stable eastern boundary was found.

If the present distribution of the grey squirrel is considered in relation to maps of the physical features of England and Wales, and a map of the heavily industrialized areas, some explanation is given for the presence of gaps in the territory of the species. This becomes clearer when a map of the

and south-westwards in the same line till Brecknockshire is reached, where the boundary falls south in a line from Brecon to Llantrisant. The territory in Denbigh and adjacent counties has presumably been colonized from the introduced squirrels released at Rossett in 1903, and from introductions at Lyme,
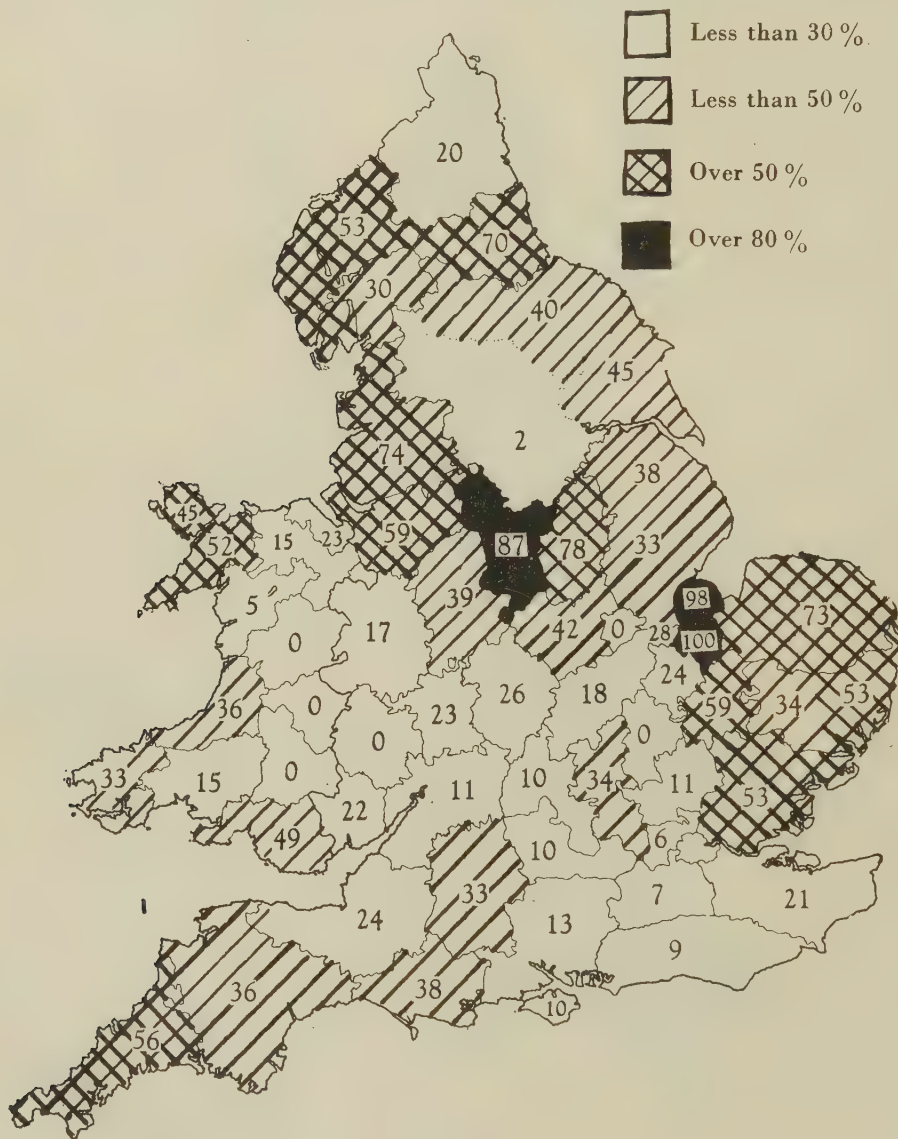
Map 2c. The percentage of covered parishes in each county reporting no squirrels.

introduction points of the species is also consulted (Middleton, 1930, Pl. 1). Apart from the eastern boundary, the main lines along which the range is halted at the present time lie, to the north, along the River Witham across Lincolnshire; along the River Trent through Nottinghamshire and Derbyshire,

Dunham, and Bramhall in Cheshire. The spread of this colony has been limited; it cannot be compared to the spread from introduction points around London, in Bedfordshire, Northamptonshire and Kent, which were presumably the starting points from which the main area to the south sprang. It is

not clear why the Denbigh squirrels did not join with the southern population through Shropshire; or why there is at present no link between it and the other grey squirrel area in Cheshire arising from introductions in that county.

The introduction at Exeter in Devonshire gave rise to the colonized area there; this appears to have spread south down the coast, but to have been prevented from any westward extension, probably by the unsuitable nature of the country; although scattered reports from other parts of the county (which proved impossible to verify) came in during this survey.

The Yorkshire distribution has remained very largely the same; a link southwards with the Lincolnshire population may be prevented by the Rivers Humber and Ouse, and by the industrial areas of the southern part of the West Riding, Derbyshire, and Nottinghamshire. The mountains and moors to the west and the industrial areas in Durham may contribute to hem in this territory which sprang from at least four introductions into the county.

The natural barriers preventing the spread of grey squirrel territory in this country therefore include large rivers with few bridges, unsuitable country (marshy or moorland, with few trees) and industrial areas. The first of these factors can sometimes be overcome; the grey squirrel has crossed the Severn in force; and grey squirrels have been observed swimming across the Wye. That it may act as a deterrent seems to be indicated in the case of the Witham and the Trent. In Lincolnshire the part of the county south of the Witham (Kesteven) has a fairly widespread grey squirrel population, reaching up to the river boundary. The first report of grey squirrels north of the river came in 1944, at a place near a bridge over it. A second crossing was reported the next year at another bridge point. Only two other parishes in Lindsey report the grey squirrel, and one of those is near the second bridgehead. In Nottinghamshire only six parishes report the grey squirrel, and all are south-east of the Trent, which crosses the county. In Derbyshire the Trent and the Derwent form a fork which separates the southern tip of the county from the north. Only one record of a grey squirrel came from north of this barrier, and six immediately south of it. A recent article in the press notes that Lancashire attributes the absence of the grey squirrel in that county to the barrier formed by the Mersey and the Pennines.

There is little doubt that large stretches of fenland, moor, or heavily industrialized country will be unsuitable for squirrels. The Isle of Ely and the fenland around the Wash report no squirrels. The southern, industrial area of Lancashire is largely devoid of the squirrel also. Derby, Norfolk, and the North Riding of Yorkshire have a large proportion of parishes reporting no squirrels.

It may be noted that it is apparently not impossibility of entry that prevents the grey squirrel from colonizing Norfolk, Suffolk, and east Essex. Introductions have been made in this area; one at Northrepps, in Norfolk; the squirrels apparently died out here. In 1937 Parsons and Middleton had reports of grey squirrels from the east coast area in both Suffolk and Essex. These squirrels have now disappeared. This suggests that the country is unsuitable for them; only two other of the thirty-three known introductions in this country failed.

It is very likely that many small introductions of the grey species have been made throughout the country, of which no record exists. The escape of grey squirrels kept as pets may well have been an important factor in the spread of the species.

(b) The grey and the red squirrel

Map 1a shows that there is still a very large area of England and Wales where the red squirrel is found. Superimposing Maps 1a and 1b the relative distribution of the two species is seen. In the areas where the grey squirrel has been for 15 years or more, 66% of the grid squares are negative for the red squirrel. This does suggest that after a time the presence of the grey squirrel results in the disappearance of the red. But the matter is confused by several factors: (1) there is no definite information on the distribution of the red squirrel in these areas prior to the coming of the grey squirrel; (2) the records of the distribution of the grey squirrel gathered in 1930 are not complete; (3) the grid system again obscures the significance—as in a square marked for the presence of the grey squirrel in 1930 there may be included parishes that were never colonized by this species, and thus could remain a stronghold of the red squirrel.

An increase in the numbers of the red squirrel has been reported from most of the Welsh counties free of the grey squirrel, with the exception of Pembrokeshire. The reasons for its decrease in this county were listed by the Pest Officer to the W.A.E.C. as follows: steel-trapping for rabbits, felling of trees and the decline of game preserves. In Scotland the Forestry Commission areas report the red squirrel populations as decreasing or not changing in numbers, areas where they are numerous are rare. This situation cannot be taken as applying to the rest of Scotland, where the position is not yet known. On Forestry Commission land there are often large areas of trees below the cone-bearing age, which would not be expected to support large numbers of red squirrels. Felling of older trees on a large scale robs the squirrel of its habitat; colonization of new plantations when the trees are of the right age is made difficult by control measures.

Generally, the wide area still populated by the red squirrel is reassuring to those who thought that the species was rapidly dying out.

5. SUMMARY AND CONCLUSIONS

1. A questionnaire survey of the distribution of the grey squirrel (*Sciurus carolinensis*) in England and Wales has been carried out for the first time since 1937. In the present survey 77 % of the total number of parishes in England and Wales were covered (9781 out of 12,780) and 1580 out of 1638 10 km. grid squares were covered, or 96 %.

2. The grey squirrel was found to be present in 708 grid squares (45 % of the total number covered) and in 2795 parishes, or 29 % of the total number of parishes covered. In 1937 it was found in 274 grid squares. 112 new squares have been added on the western boundary of the distribution.

3. The eastern boundary of the grey squirrel has not changed markedly from the 1937 position. The reason for this limit is not known. In some other areas grey squirrels may be halted in their spread across country by such natural barriers as large rivers with few bridges, and by mountainous or treeless country.

4. This survey is the first attempt to find out with accuracy the distribution of our native red squirrel (*S. vulgaris leucourus*). The results are encouraging in that they show a wider range than was expected; but no indication of density is given. The red squirrel was reported from 1011 grid squares (64 % of total covered) compared with the grid-square percentage of 45 for grey squirrels. The number of parishes reporting the red squirrel was 2316, 24 % of the total

number of parishes covered. Again, this may be compared with the corresponding grey squirrel figure of 29 %. From this comparison it will be seen that the red squirrel is present in 19 % more grid squares than the grey squirrel, but in 5 % less of the parishes. The conclusion that may be drawn is that the red squirrel is more widely and thinly distributed.

5. There is an indication that after a period of 15 years or more the presence of the grey species may result in the disappearance of the red squirrel. Of squares occupied by the grey squirrel in 1930, 66 % now have no grey squirrels.

6. 401 squares (25 % of total number covered) and 1182 parishes (12 % of total number covered) now contain both species.

7. Absence of squirrels of both species was reported for 262 squares and 3482 parishes (16 % and 36 % of the total number covered). The usual apparent causes for the absence of squirrels in an area were found to be lack of sufficient trees in fen, moorland, coastal or heavily industrialized areas.

8. The survey was more accurate, and more parishes were covered, than at first seemed likely. 12,780 parishes were sent questionnaires, and 9781 replied. 1580 10 km. grid squares were covered—an area of 15,800 sq.km. It would have been impossible to cover this area personally in 1 year; and untrained observers had to be used. Because of this, simplified questionnaire forms were used, and no data on density or fluctuations in numbers could be obtained for the whole country. The survey will, it is hoped, be of value in providing a basis for future study of the effect of the grey squirrel on our native red squirrel, and in following the further spread of the introduced species.

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THE SEASONAL ABUNDANCE OF BLOOD-SUCKING FLIES IN A GRASSED WOODLAND AREA IN CENTRAL TANGANYIKA

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(With 2 Figures in the Text)

1. INTRODUCTION

Mpwapwa, lat. 6° S., long. 37° E., altitude 3350 ft., has an average annual rainfall of 26 in., all of which falls between December and April. The observations considered in this paper were made in the Kikombo valley, which is enclosed by steep hills rising to 6000 ft. above sea-level. A number of permanent streams descend from these high hills, but in the dry season all disappear soon after reaching the flats. The Veterinary Department has a farm in the valley.

In an attempt to discover in which parts of the bush surrounding the farm the tsetse fly *Glossina pallidipes* Austen was lurking, a number of 'fly-rounds' were laid out. A 'fly-round' is a path passing through the terrain under investigation, along which at regular intervals, usually once a week, a party of three trained Africans (equipped in this case with a bait ox) proceeds, catching such flies as appear to them. These Kikombo fly-rounds were for the purpose of investigating *G. pallidipes* and the observations on other flies, recorded in this paper, were made only incidentally. Had the investigation of Tabanidae, etc., been a primary objective the fly-rounds would have been sited differently—in particular a high-altitude round would have been included.

2. THE FLY-ROUNDS

The catches from four fly-rounds are presented here. The Chibwesangula Round (10,930 yd.) begins in the Kikombo valley, goes over the pass at the east end of the valley into a region of 'miombo' (open *Brachystegia* wooding) with dry thicket, thicketed dry streams and patches of cultivation. The Bomba Round (4580 yd.) follows the Mpwapwa River (one of the permanent streams mentioned above) though it does not pass through the evergreen riverine forest. The Kigute Round (11,150 yd.) explores the valley of Buffalo Creek, and for part of its length is near that permanent stream. The Kiboriani Round (4840 yd.) taps much the same area as the Bomba Round, but at a greater altitude.

Hippobosca longipennis and a number of Tabanidae were taken regularly. Records were kept of *H. longipennis* and the commoner Tabanidae from July 1940 to December 1942, except that the records for January and February 1942 are missing. The only common biting fly which was not recorded was *Stomoxys*. From January 1943 to February 1944 notes were kept of the presence or absence of certain species, and from these notes the two right-hand columns of the following table of flight seasons were compiled. Unfortunately, in these notes all species of *Tabanus* and all species of *Haematopota* were grouped together, so that information on the flight seasons of the species of these two genera is restricted to 1940–2.

Hippobosca is viviparous, with a life history essentially similar to that of tsetse, and consequently its flying population does not show enormous variations in the course of a year (Fig. 1). Tabanidae are oviparous, and the larvae are all more or less aquatic, and as with other insects with aquatic larvae there is a tendency to have a short 'flight season', when all the individuals are adult, and a longer off season when adults are absent.

The 'Pangoninae' in Mpwapwa is a group of about six species not easily distinguished (but see remarks on the next page).

3. FLIGHT SEASONS

	1940	1941	1942	1943	1944
Mesomyia fallax Austen	Aug.–	Jan. July–Dec.	Aug.–Dec.	Aug.–Nov.	
'Pangoninae'		Mar.–May	Mar.–June	Mar.–May	
Phara speciosa Austen		Jan.	Dec.	Jan. Mar.	Jan.–Feb.
Tabanus atrimanus Loew	Sept.–	Apr. Sept.–	May Oct.–	?	
T. insignus Loew	Aug.–	June Nov.–	May Oct.–	?	
T. maculatissimus Macquart	July–	June Oct.–	? Nov.–	?	
T. taeniola Palisot de Beauvois	Nov.–	June Oct.–	July Oct.–	?	
Haematopota mactans Austen⎱ *H. vittata* Loew⎰	Oct.–	June Oct.–	July July–?, Sept.–	?	
H. nobilis Grünberg disappeared during only two months, Sept. and Oct. 1941					
Haematopota spp.	Oct.–	July Nov.–	Aug. Dec.–	?	
Hippobosca longipennis Fabricius was always present					

[The following species were seen by me, and Mr Oyeuch's identifications therefore confirmed as correct: *Phara speciosa, Tabanus atrimanus, T. insignis, T. taeniola, Haematopota mactans, H. nobilis* and *Hippobosca longipennis*; of the remainder, the 'Pangoninae' probably consisted of a mixture of *Dorcalaemus compactus* Austen, *Pangonius oldii* Austen, *Nuceria neavei* Austen and at least two other species whose identity is uncertain; *Mesomyia fallax* and *Tabanus maculatissimus* are both very distinctive and unmistakable forms, and have, together with the

under these two names; *Haematopota* spp. refer to various *Haematopota* other than the above species, and include *H. abyssinica* Surcouf and *H. pertinens* Austen, and possibly other species not now determinable. (W. H. Potts.)]

4. ABUNDANCE* IN TIME AND PLACE

The Appendix gives the mean monthly catches, expressed in terms of numbers of the various species caught per 10,000 yards, on the four rounds, together with the mean of the four rounds, giving a
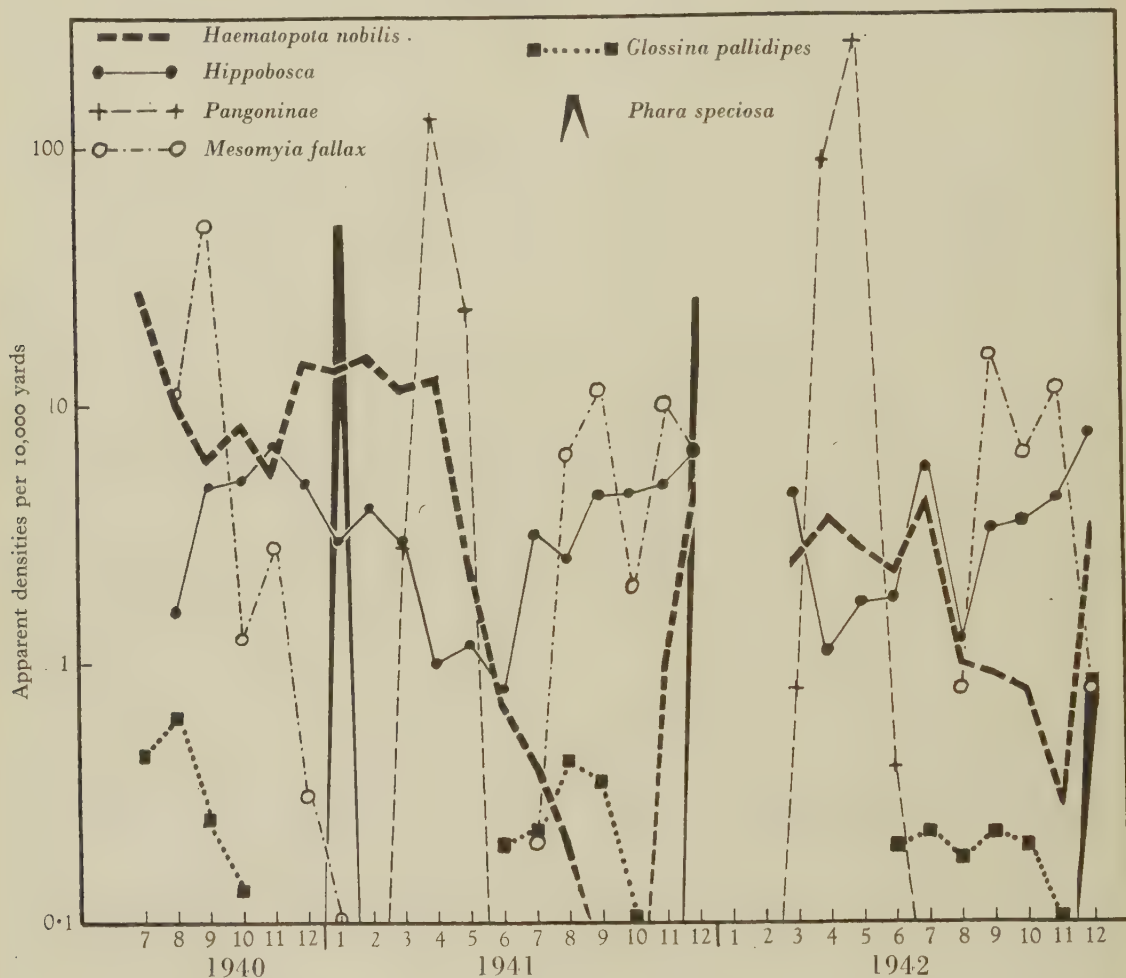
Fig. 1.

various Pangonines cited above, and the two *Haematopota* to be mentioned next, been collected by me in the precise area referred to, so that, though I have not actually seen the specimens collected by him, I am confident that the identifications made by Mr Oyeuch can be regarded as correct; *H. vittata* can rather resemble *H. mactans* so that I consider it preferable to combine the flight seasons recorded

figure more or less representative of the whole valley. This last figure is derived directly from the means for the rounds, i.e. it gives an answer as

* 'Abundance' here is actually 'apparent density' determined by counts along line transects, in the sense used by tsetse investigators; relative abundance or availability of possibly preferred hosts at different seasons may affect these figures.

though all the rounds were the same length and done the same number of times. From these means for the whole valley the graphs (Figs. 1 and 2) are drawn (logarithmic scale). The figures of the catches of *Glossina pallidipes* Austen are also given, these being the totals of both sexes caught. The catches of other flies were exclusively females as the males do not suck blood and were not attracted to the bait ox. The 'totals' at the feet of the columns indicate the relative abundance of the various species on each

reflexion of their nearness to the breeding grounds of the flies. The distribution of the 'Pangoninae' is a little peculiar; it may be that the Kiboriani Round taps a specially favoured breeding ground, and that for the rest they are such strong fliers that they distribute themselves more or less evenly over the whole valley. That *Hippobosca longipennis* should be concentrated near streams is unexpected, as its breeding is independent of water; the concentration, however, is not very marked.
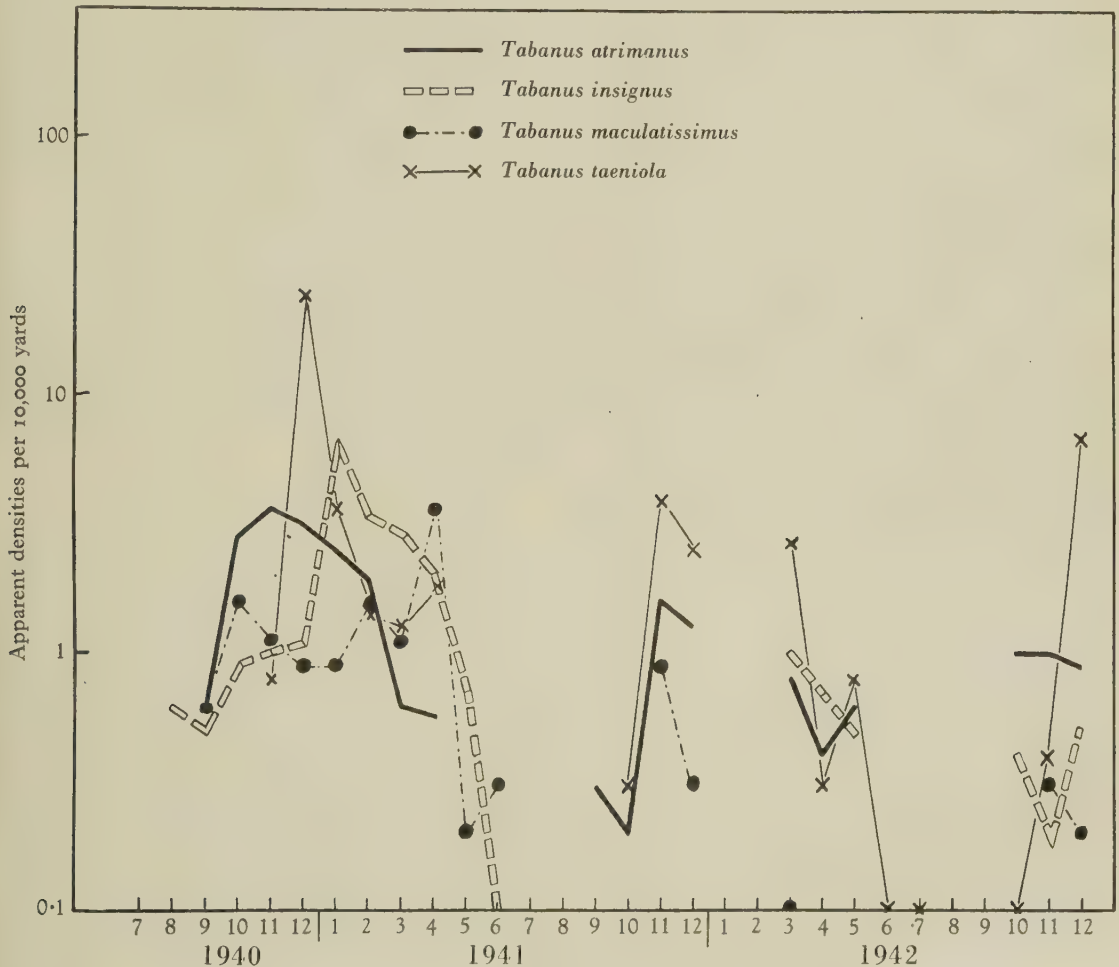

Fig. 2.

round. With the exception of 'Pangoninae' and *G. pallidipes*, every species is most abundant on the Bomba or Kiboriani Round, least abundant on the Chibwesangula Round, with the Kigute Round intermediate. The Bomba and Kiboriani Rounds lie nearest to permanent water, and the Chibwesangula Round farthest from it, and no doubt the greater abundance of Tabanidae on the former rounds is a

5. NUMBER OF GENERATIONS PER YEAR

Study of the graphs emphasizes what is apparent also from the table above—that different species may be classed in three ways: those with a very short flight season, those with a very long flight season, and those in between. Of those with a very short season, there can be little doubt that *Phara speciosa* has but a single generation per year, while the season

of the 'Pangoninae' is also so short that it is very probable that each single species within this group has but one generation per year.

Of those with a prolonged flight season the most notable example is *Haematopota nobilis* (Fig. 1) which was present throughout the 30 months except September and October 1942. This species would appear normally to have a succession of generations throughout the year, and its disappearance in September and October 1942, while possibly due to some unusual weather conditions, may equally be due to two generations fortuitously synchronizing.

The other species considered all have a more or less prolonged flight season complemented by a complete off-season of one or more months each year. Whether this indicates a life-cycle of one year, with a prolonged and irregular emergence period, or whether several generations occur during the flight season, followed by a period during which the larva develops slowly or goes into a resting stage, cannot be made out from the present data. It is noteworthy, however, that *Mesomyia fallax* regularly has two peaks of population in September and November, and a probable life history is as follows: eggs laid in November give rise to adults emerging in September—eggs laid in September give rise to adults emerging in November. The apparent regularity with which *Mesomyia fallax* has maxima in September and November every year is not followed by the other species considered, which have their maxima in different months, and slightly different flight seasons, each year.

The only species in common with Vanderplank's observations of 1940 is *Tabanus taeniola*. This had the same flight season, November–June, and maximum in the same month, December, in Shinyanga as in Mpwapwa, although subsequent years in Mpwapwa showed differences in both these respects (Fig. 3). Mpwapwa is 250 miles south-east of Shinyanga.

6. REVIEW OF THE LITERATURE

Irregular behaviour of this type is familiar in Tabanidae elsewhere. Thus in Arkansas (Schwardt, 1931, 1932, 1935) *Tabanus atratus* F. has one generation a year and flies in June and July; *T. lineola* F. has two generations a year and flies from June till August; *T. sulcifrons* Macq. has one generation a year and flies in late August and early September. In Pennsylvania (Frost, 1936) *T. atratus* F. flies June–September, *T. sulcifrons* Macq. July–August, *T. lasiopthalmus* Macq. May–June, *T. giganteus* De G. late September to early October. In the Philippines (Monresa & Mondoñedo, 1935) *Tabanus striatus* F. is present throughout the year. In India (Isaac, 1932, 1933) *Haematopota roralis* F. and *Tabanus speciosus* Ric. each have three broods a year and an off-season of six months.

7. RELATION TO TRYPANOSOMIASIS

The Kikombo valley was once free of cattle trypanosomiasis. When the disease first appeared it was considered to be mechanically transmitted by flies. Later *Glossina pallidipes* was discovered in the valley, the hypothesis of mechanical transmission was tacitly abandoned, and as *G. pallidipes* was reduced so was the incidence of trypanosomiasis reduced. Yet the densities of blood-sucking flies recorded above are high and sustained, and at first sight it appears strange that the veterinary stock does not suffer more from mechanically transmitted trypanosomiasis. One of the species present, *Tabanus taeniola* is considered the chief vector in the Sudan of *Trypanosoma soudanense* (Bennett, 1929). A possible explanation of this anomaly would be that mechanical transmission can only take place between animals which are close together. The cattle are not herded close enough to game to enable mechanical transmission to occur from game to cattle. Once trypanosomiasis is established in the herd by *Glossina* it could be spread mechanically within the herd by Tabanidae, but probably at Mpwapwa the fly-struck beasts would be detected and treated before the outbreak spread very far.

8. INDICATOR SPECIES

The suggestion had been made, in the Tsetse Research Department, that, in our work generally, more attention should be paid to insects other than tsetses, in the hope of discovering 'indicator species' which would point the way to an understanding of tsetse distribution and activity. An obvious group with which to start was other blood-sucking flies, and this was one reason for making the observations here recorded.

That the catches of *Glossina pallidipes* show no correspondence with those of any of the other species caught is not important, for *G. pallidipes* was even in 1940 approaching extinction in the valley. But the data presented show that the size of a catch of any Tabanid in any place at any time is determined to a very large extent by two considerations: the season of the species and the distance from a breeding-place of the species. Neither of these considerations is relevant to catches of tsetses, and it seems clear that 'indicator species' will not be found among Tabanidae.

Hippobosca longipennis suffers from another disability. All the species of this genus seem to be especially associated with one particular host, and the variations in catches of *H. longipennis* recorded in Fig. 1 are more likely to be reflections of the movements of wild felines than of anything else.

9. ACKNOWLEDGEMENTS

10. SUMMARY

1. Records are presented of catches of *Hippobosca longipennis* and a number of Tabanidae over 30 months, 1940–2.

2. All species were taken in greater numbers near streams.

3. All Tabanidae have a 'flight season' when adults are found, and an off-season when they are not.

4. *Phara speciosa* and the Pangoninae appear to have but one generation a year in Mpwapwa. *Mesomyia fallax* probably has two. The other Tabanidae may have several.

5. Maximum numbers of adults of a particular species do not normally occur in the same month in subsequent years, nor do the flight seasons exactly coincide in subsequent years.

6. Possibilities of mechanical transmission of cattle trypanosomiasis are discussed.

7. The possibility of using other biting flies as indicators for *Glossina* spp. is considered, but, mainly on account of paras. 2 and 3 above, it is concluded that no 'indicator species' will be found among Tabanidae. *Hippobosca* spp. are also unsuitable.

APPENDIX

Apparent densities per 10,000 yd. (monthly means)

Glossina pallidipes

	Chibwesangula	Bomba	Kigute	Kiboriani	Mean
1940					
7	0·2	0·7	0·9	—	0·45
8	—	1·0	0·9	0·7	0·65
9	0·7	—	—	0·3	0·25
10	—	0·3	0·2	—	0·13
11	—	—	—	—	—
12	—	—	—	—	—
1941					
1	—	—	—	—	—
2	—	—	—	—	—
3	—	—	—	—	—
4	—	—	—	—	—
5	—	—	—	—	—
6	0·3	—	0·5	—	0·2
7	—	—	1·0	—	0·25
8	—	0·7	1·0	—	0·43
9	0·2	—	0·6	0·7	0·38
10	—	—	0·1	—	0·03
11	—	—	—	—	—
12	—	—	—	—	—
1942					
1	—	—	—	—	—
2	—	—	—	—	—
3	—	—	—	—	—
4	—	—	—	—	—
5	—	—	—	—	—
6	0·5	—	0·3	—	0·2
7	0·2	—	0·7	—	0·23
8	0·5	—	0·2	—	0·18
9	—	—	0·9	—	0·23
10	—	0·7	0·1	—	0·2
11	—	—	0·3	—	0·08
12	—	—	—	—	—
Totals	2·6	3·4	7·7	1·7	

Maximum density recorded on any one day: 2·7 (Kigute)

Apparent densities per 10,000 yd. (monthly means)

	Mesomyia fallax					'Pangoninae'					Phara speciosa				
	Chibwesangula	Bomba	Kigute	Kiboriani	Mean	Chibwesangula	Bomba	Kigute	Kiboriani	Mean	Chibwesangula	Bomba	Kigute	Kiboriani	Mean
1940															
7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8	16	21	10	23	11	—	—	—	—	—	—	—	—	—	—
9	7	100	7	83	52	—	—	—	—	—	—	—	—	—	—
10	11	15	25	20	12	—	—	—	—	—	—	—	—	—	—
11	—	17	0·3	57	27	—	—	—	—	—	—	—	—	—	—
12	—	—	—	1	0·3	—	—	—	—	—	—	—	—	—	—
1941															
1	—	0·4	—	—	0·1	—	—	—	—	—	2·7	87·3	42·0	69·0	50
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3	—	—	—	—	—	2·5	2·7	2·0	4·0	2·8	—	—	—	—	—
4	—	—	—	—	—	103	71	102	233	127	—	—	—	—	—
5	—	—	—	—	—	2·4	19·7	12·0	59·0	23·3	—	—	—	—	—
6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7	0·7	—	—	—	0·2	—	—	—	—	—	—	—	—	—	—
8	8	3	4	11	7	—	—	—	—	—	—	—	—	—	—
9	8	4	5	29	12	—	—	—	—	—	—	—	—	—	—
10	2	2	1	3	2	—	—	—	—	—	—	—	—	—	—
11	6	15	10	10	10	—	—	—	—	—	—	—	—	—	—
12	6	5	5	8	6	—	—	—	—	—	—	—	—	—	—
1942															
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3	—	—	—	—	—	0·5	2·2	0·3	—	0·8	—	—	—	—	—
4	—	—	—	—	—	11	2	107	226	86	—	—	—	—	—
5	—	—	—	—	—	256	205	56	517	259	—	—	—	—	—
6	—	—	—	—	—	0·5	—	1·0	—	0·4	—	—	—	—	—
7	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—
8	16	2	1	25	15	—	—	—	—	—	—	—	—	—	—
9	11	17	3	3	6	—	—	—	—	—	—	—	—	—	—
10	4	4	8	15	12	—	—	—	—	—	—	—	—	—	—
11	—	9	19	—	—	—	—	—	—	—	—	1	—	—	1
12	—	1	2	—	1	—	—	—	—	—	3	21	12	60	24
Totals:	97	214	100	288		376	303	280	1039		9	109	54	129	

Maximum density recorded on any one day: 201 (Bomba)

Maximum density recorded on any one day: 1478 (Kiboriani)

Maximum density recorded on any one day: 201 (Bomba)

Apparent densities per 10,000 yd. (monthly means)

	Tabanus atrimanus					Tabanus insignus				
	Chibwesangula	Bomba	Kigute	Kiboriani	Mean	Chibwesangula	Bomba	Kigute	Kiboriani	Mean
1940										
7	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	2·2	—	—	0·6
9	—	1·4	—	1·0	0·6	—	1·6	0·2	—	0·5
10	—	4·4	1·2	6·0	2·9	—	1·6	—	2·0	0·9
11	0·3	3·9	4·6	6·0	3·7	—	1·5	1·3	1·0	1·0
12	—	5·8	0·3	7·0	3·2	0·2	1·8	0·3	2·0	1·1
1941										
1	0·5	6·6	0·8	2·0	2·5	0·7	12·0	2·0	8·0	5·7
2	0·3	4·4	1·0	2·0	1·9	0·9	5·7	1·0	6·0	3·4
3	—	2·2	0·3	—	0·6	0·9	2·7	2·0	6·0	2·9
4	—	—	1·0	1·0	0·5	2·7	1·5	1·0	3·0	2·1
5	—	—	—	—	—	1·2	0·7	1·0	—	0·7
6	—	—	—	—	—	—	—	0·4	—	0·1
7	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	—	—	—	—
9	—	—	—	1·0	0·3	—	—	—	—	—
10	—	0·5	0·4	—	0·2	—	—	—	—	—
11	—	1·5	2·0	3·0	1·6	—	0·7	0·4	—	0·3
12	0·3	0·7	3·0	1·0	1·3	—	—	—	—	—
1942										
1	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—
3	—	2·2	1·0	—	0·8	1·8	—	1·0	1·0	1·0
4	—	—	0·2	1·0	0·3	1·4	—	0·2	1·0	0·7
5	—	1·1	0·4	1·0	0·6	—	1·1	—	1·0	0·5
6	—	—	0·1	—	—	—	—	0·1	—	—
7	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—	—
10	—	2·9	1·0	—	1·0	—	1·5	—	—	0·4
11	0·5	0·5	1·0	2·0	1·0	—	0·5	0·2	—	0·2
12	—	0·4	2·0	1·0	0·9	—	1·1	1·0	—	0·5
Totals:	2	39	20	35		10	36	12	31	

Maximum density recorded on any one day: 17 (Kiboriani)   Maximum density recorded on any one day: 20 (Bomba)

Apparent densities per 10,000 yd. (monthly means)

	Tabanus maculatissimus					Tabanus taeniola				
	Chibwesangula	Bomba	Kigute	Kiboriani	Mean	Chibwesangula	Bomba	Kigute	Kiboriani	Mean
1940										
7	0·2	—	—	—	0·1	—	—	—	—	—
8	—	—	0·1	—	—	—	—	—	—	—
9	0·2	1·9	0·4	1·0	0·6	—	—	—	—	—
10	—	4·1	0·1	2·0	1·6	—	—	—	—	—
11	—	1·1	0·5	3·0	1·2	—	1·1	—	2·0	0·8
12	—	1·5	—	2·0	0·9	15	41	3	36	24
1941										
1	—	1·1	0·4	2·0	0·9	2·3	2·9	3·0	6·0	3·6
2	0·3	2·6	1·0	2·0	1·5	1·2	2·2	1·0	2·0	1·6
3	—	2·2	1·0	1·0	1·1	0·9	2·2	1·0	1·0	1·3
4	—	0·7	0·2	14·0	3·7	2·1	2·9	1·0	1·0	1·8
5	0·3	—	0·3	—	0·2	—	—	—	—	—
6	—	—	0·3	1·0	0·3	—	—	0·1	1·0	0·3
7	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	—	0·1	—	—
9	—	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—	—	1·0	0·3
11	—	1·5	0·1	2·0	0·9	1·8	8·0	0·6	5·0	3·9
12	—	—	0·3	1·0	0·3	1·8	3·3	2·0	3·0	2·6
1942										
1	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—
3	—	—	0·2	—	0·1	6·9	—	3·0	1·0	2·7
4	—	—	—	—	—	0·9	—	0·4	—	0·3
5	—	—	0·1	—	—	—	2·2	1·0	—	0·8
6	—	—	0·1	—	—	—	—	0·3	—	0·1
7	—	—	—	—	—	—	—	0·5	—	0·1
8	—	—	—	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	0·5	—	—	—	0·1
11	—	—	0·1	1·0	0·3	—	0·5	—	1·0	0·4
12	—	0·4	0·4	—	0·2	3·7	8·4	3·0	12·0	6·8
Totals:	1·0	17	6	32		37	75	20	72	

Maximum density recorded on any one day: 21 (Kiboriani)   Maximum density recorded on any one day: 101 (Bomba)

Apparent densities per 10,000 yd. (monthly means)

	Haematopota mactans					Haematopota vittata					Haematopota nobilis				
	Chibwesangula	Bomba	Kigute	Kiboriani	Mean	Chibwesangula	Bomba	Kigute	Kiboriani	Mean	Chibwesangula	Bomba	Kigute	Kiboriani	Mean
1940															
7	—	—	—	—	—	—	—	—	—	—	2	48	5	52	27
8	—	—	—	—	—	—	—	—	—	—	1	18	4	20	11
9	—	—	—	—	—	—	—	—	—	—	—	10	1	14	6
10	—	2·5	2·2	0·4	1·3	—	—	1·5	3·0	1·1	1	13	6	13	8
11	0·6	7·0	2·5	5·0	3·8	0·3	37	19	30	21	—	9	6	8	6
12	0·9	5·5	4·8	5·0	4·0	10	66	11	40	32	1	30	3	24	14
1941															
1	0·9	0·7	0·1	1·0	0·7	20	114	30	70	58	1	22	3	30	14
2	—	—	0·4	—	0·1	11	39	10	27	21	—	25	2	34	15
3	1·1	—	0·3	—	0·3	—	—	0·6	—	0·2	—	10	6	30	12
4	—	0·7	—	—	0·2	—	—	—	1·0	0·3	—	15	5	28	12
5	—	—	2·0	—	0·5	—	—	—	1·0	0·3	—	2	2	5	2
6	0·3	3·3	1·0	1·0	1·4	—	—	—	—	—	—	1	1	1	1
7	—	—	—	—	—	—	—	0·1	—	0·1	—	2	—	—	0·4
8	—	—	—	—	—	—	—	—	—	—	—	0·7	—	—	0·2
9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10	—	—	0·3	—	0·1	—	—	—	—	—	—	—	—	—	—
11	0·3	2·9	6·0	11·0	5·1	—	—	—	—	—	—	1	—	3	1
12	6·0	22·0	12·0	5·0	11·0	—	—	—	—	—	—	8	3	7	5
1942															
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3	1·8	2·2	2·0	—	1·5	—	2·2	1·0	1·0	0·8	—	4	3	3	3
4	—	—	1·0	—	0·3	—	—	1·0	1·0	0·5	—	10	4	10	4
5	—	—	3·0	1·0	1·0	—	—	1·0	—	0·5	—	2	3	6	3
6	0·5	2·2	5·0	3·0	2·7	—	—	—	—	—	—	2	5	2	2
7	—	—	2·0	—	1·1	—	—	0·3	—	0·1	—	4	3	4	3
8	—	—	0·1	—	—	—	—	0·4	—	0·1	—	2	1	1	3
9	—	—	0·2	—	0·1	—	—	0·3	—	0·1	—	2	1	1	1
10	—	0·7	—	—	0·2	—	—	—	1·0	0·3	—	3	—	1	1
11	—	1·1	1·0	—	0·5	—	—	—	—	—	—	1·1	—	—	0·3
12	—	—	1·0	8·0	2·3	—	0·7	—	—	0·4	—	3	1	9	3
Totals:	13	53	47	40		41	259	76	176		6	238	67	305	

Maximum density recorded on any one day: 52 (Bomba)

Maximum density recorded on any one day: 242 (Bomba)

Maximum density recorded on any one day: 93 (Kiboriani)

Apparent densities per 10,000 yd. (monthly means)

	Haematopota spp.					Hippobosca longipennis				
	Chibwesangula	Bomba	Kigute	Kiboriani	Mean	Chibwesangula	Bomba	Kigute	Kiboriani	Mean
1940										
7	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	0·9	2·2	0·4	3·0	1·6
9	—	—	—	—	—	1·8	11·2	2·6	4·0	4·9
10	—	1·1	1·3	1·0	0·9	1·5	13·1	2·2	4·0	5·2
11	9·5	38·0	17·0	27·0	23·0	3·7	13·5	3·8	6·0	6·8
12	53·0	159·0	51·0	102·0	91·0	4·6	10·6	1·8	3·0	5·0
1941										
1	6·9	23·0	19·0	33·0	21·0	2·5	3·3	4·0	2·0	3·0
2	5·8	43·5	6·0	16·0	17·8	2·4	7·0	3·0	4·0	4·1
3	3·9	7·7	10·0	4·0	6·4	2·1	4·4	0·6	5·0	3·0
4	2·1	6·6	3·0	3·0	4·0	0·9	2·9	0·2	—	1·0
5	1·5	—	1·0	—	0·6	—	2·9	2·0	—	1·2
6	—	—	0·3	—	0·1	0·6	1·1	2·0	—	0·9
7	—	—	0·4	—	0·1	1·6	8·0	2·0	1·0	3·2
8	—	—	—	—	—	0·9	3·6	2·0	4·0	2·6
9	—	—	—	—	—	3·2	6·5	4·0	5·0	4·7
10	—	—	—	—	—	2·9	5·5	3·0	7·0	4·6
11	1·2	1·5	2·1	15·0	5·0	5·2	4·4	6·0	4·0	4·9
12	41·0	60·0	44·0	70·0	53·8	6·1	7·3	6·0	7·0	6·6
1942										
1	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—	—	—	—
3	—	—	3·3	—	0·8	6·4	6·5	4·0	2·0	4·6
4	—	—	4·2	2·0	1·6	0·5	—	2·0	2·0	1·1
5	—	2·2	3·0	—	1·3	0·5	2·2	2·0	2·0	1·7
6	—	—	5·0	—	1·3	0·5	2·2	2·0	3·0	1·9
7	—	1·1	3·0	—	1·0	1·1	13·1	1·0	7·0	5·6
8	—	—	1·0	—	0·3	0·9	—	1·0	3·0	1·2
9	—	—	0·4	—	0·1	0·9	4·4	2·0	6·0	3·3
10	—	—	0·4	—	0·1	3·2	2·9	3·0	5·0	3·5
11	—	2·1	0·3	—	0·6	1·4	8·2	2·0	6·0	4·4
12	—	11·3	3·0	13·0	6·8	3·7	9·5	5·0	12·0	7·6
Totals:	125	357	179	286		60	157	70	107	

Maximum density recorded on any one day: 26 (Bomba)

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(With the exception of the last one on the list, these papers have been seen by the author only as abstracts in the *Review of Applied Entomology*. References have been checked to the originals by Mr W. H. Potts.)

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REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 32, No. 2, 1945; and Vol. 33, No. 1, 1945)

The second number of the *Journal of Ecology*, Vol. 32, contains six original papers, three parts of the Biological Flora and one review.

Four of the original papers are vegetation studies, the first by C. P. Petch deals briefly with the heath vegetation of Roydon Common, Norfolk. It is followed by a study of Cader Idris and Craig-y-Benglog by E. Price Evans, in which the influence of rock composition on the distribution of the flora is described. Ian Hepburn gives an account of the vegetation of the sand dunes of the Camel Estuary, North Cornwall, including also a comparison with other dune areas. M. Zohary gives a general outline of the vegetation and soils in Wada Araba, in the Near East. The remaining papers include an account of the peat and vegetation of Figyn Blaen Brefi, a Welsh upland bog, by E. G. Davies, and its relation to topography, pollen analyses being included. R. Laird deals with the influence of soil reaction on rotation grass and on the effect of this fact on grasslands developing from different seed mixtures. There is a review on Erdtman's book on Pollen Analysis by V. M. Conway.

The Biological Flora is continued by the studies of *Acer, A. pseudo-platanus, A. campestris* and *A. platanoides.*

Vol. 33, No. 1, of the *Journal* deals more largely with foreign ecology, to which three of the five original papers refer. There are three parts of the Biological Flora and four reviews.

The first paper, by J. S. Beard, records the chief stages in plant succession on the volcanic cone of the Soufriere in St Vincent. It is followed by an account of the influence of the human factor in tropical plant ecology by A. S. Thomas, described particularly in reference to the hillside vegetation in Uganda. Nicholas Polunin records the salient features of plant life in the Kongsfjord (King's Bay), West Spitsbergen. British ecology is represented by the sixth and last report of the transplant experiments at Potterne, carried out for the British Ecological Society by E. M. Marsden-Jones and W. B. Turrill. There is also a full account by E. W. Jones of the conditions under which Douglas Fir regenerates in the New Forest.

The Biological Flora parts included are by N. W. Simmonds and deal with *Polygonum, P. persicaria, P. lapathifolium* and *P. Betecticale.*

The number also contains reviews dealing with recent papers on soils and vegetation in Ceylon by T. E. T. Bond, the *Journal of Animal Ecology* and two books. There is a summary of the Symposium on the 'Ecology of closely allied species', and also a list of recent papers on plant ecology. W. S. PEARSALL

THE ECOLOGY OF EELS

Léon Bertin (1942). *Les Anguilles. Variation— Croissance—Euryhalinité—Toxicité—Hermaphrodisme juvénile, Sexualité—Migrations—Metamorphoses.* 218 pp., 8 plates, 54 text-figures. Payot, 106 Boulevard St Germain, Paris. Price 50 fr.

It is just half a century since Grassi and Calandruccio established the fact that the little fish, *Leptocephalus brevirostris* captured in the Straits of Messina was the larval form of the fresh-water eel, *Anguilla anguilla.* Before and since this fundamental discovery the mystery surrounding the life history of the eel and the economic importance of eel fisheries has lead to much investigation of the biology of this extraordinary fish. The knowledge gained, published in many and various periodicals, was presented in a summarized form by Walter in *Der Flussaal* in 1910 and later by Ehrenbaum in *Der Handbuch der Binnenfischerei Mittel-europas* in 1929; both books deal with the fisheries as well as the fish. Since the latter date research on the biology of the eel has continued, the histology and physiology of the fish and the features associated with its seaward migration having in particular claimed attention. Monsieur Bertin's book presents an up-to-date account of the vast and varied knowledge now accrued about the European eel and contains a useful chapter on the eels of the world. This digest of innumerable published works which cover many lines of research, the majority of which are in German, Italian and French, will be appreciated by many zoologists, it will constitute a most useful reference book for the specialist, who will be grateful for the bibliography at the end of each chapter, and the general reader will find *Les Anguilles* eminently readable. The book is primarily a record of all that is known about the eel from its birth in the Sargasso Sea until its death years later in that place, with all the facts relevant to any particular aspect of the subject most ably set out and summarized. The author has, however, realized the limits of the type of book he has written and has refrained, wisely in view of the controversial character of much of the information available, from any argument or speculation.

The sub-titles of the book give an idea of the subjects covered and of its comprehensive character. The story of the *Leptocephalus*, its migration and metamorphosis, is fully given, all the essential details of the great discoveries of Dr Johannes Schmidt being presented and their incalculable value recognized. (It is curious, however, that in the bibliography given of Schmidt's works there is no reference to the paper in the *Philosophical Transactions of the Royal Society* of 1922 in which the first full account appeared of the breeding places of the eel.) The ascent of

the elvers into fresh water (*montée*) and the various tropisms which govern this movement are dealt with quite fully.

The life of the yellow eel, about which much is known, is given in some detail. The environmental factors influencing growth in fresh water are noted and considered, including the effect of food; in presenting the latter, the author, however, makes no mention of the organisms which compose the diet of the eel. There is one period in the life of the yellow eel about which little appears to be known, namely that time covering approximately its first six years in fresh water, when the fish is less than 35 cm. long and is often called a 'snig'. Little, apart from that recorded by Swedish workers, appears to be known about the feeding habits and movements of 'snigs'. It has been observed that they migrate up stream in large numbers and cover considerable distance: a knowledge of these movements would be of much intrinsic interest and would perhaps throw light on the seaward migration of silver eels. An excellent chapter on 'Hermaphrodisme Juvénile et Sexualité' deals with that involved and debatable question the nature and form of the sex organs of the yellow eel, a subject which has prompted investigation and discussion since Mondini's discovery in 1777 of the ovaries. In recent years knowledge of the early stages of differentiation of the gonads has been considerably increased by histological and experimental methods of study and the question of the influence of the environmental and somatic factors in determining sex can now be discussed upon more evidence and less speculation.

Interest in the silver eel lies principally in these characteristics which are associated with its seaward migration, the routes followed by migrants from different countries, the environmental conditions correlated with migration and the physiological and morphological characteristics of the eel at this time. The enlarging of the eye and the silver colouring of the belly were established as the livery of the seaward migrating eel by Petersen in 1896; to-day the physiology responsible for these changes is being studied. Investigation of the form and function of the gonads of yellow and silver eels, and of the glands of internal secretion, the inducement of migration characteristics by means of injection of hormones have all offered a promising field of research to students of the eel and of animal migration. This work is of recent date and results are necessarily few but they are encouraging and of much zoological interest. It has long been known that the migration of the eel is influenced by certain conditions of the external environment, particularly light and the amount of water. It is clear, however, that such 'tactismes migrateurs' are complex and that there is still much to learn about them.

Fisheries for silver eels, being outside the scope of the book, are described only in so far as they contribute to our knowledge of the migration habits of the fish. The author ends his book with an account of the geographical distribution of the different species of eels of the world and mentions various hypotheses which have been put forward to explain it.

Les Anguilles is a war-time production and thus the paper is of indifferent quality with the result that the reproduction of both text and figures has suffered, but the book remains a most useful and timely production.

WINIFRED E. FROST

ECOLOGY AND HISTORY

Ellsworth Huntington (**1945**). *Mainsprings of civilization.* 660 pp., 83 text-figures. John Wiley and Sons, Inc., New York; Chapman and Hall, Ltd., London. Price $4·75.

Is Dr Huntington a geographer, an historian, an economist, an anthropologist, an ethnologist, a climatologist, an explorer or an ecologist? His versatility is almost bewildering; he is one of the few geographers who has specialized in being general.

Mainsprings of civilization is the essence of Huntington's many books and publications of the last forty years. He has included what he believes to be his own most significant ideas; besides, 'it attempts to summarize the best thought of many minds'. Summarize is the word, for this stimulating, exciting book is emphatically not a synthesis. His ideas and notions and suggestions are thrown out— indeed, shot out, in all directions; there is little attempt to build a great pyramid of them—indeed, as far as one can detect, little effort to build anything with them at all. It would seem that Huntington is interested in human mental activity, in mental ingenuity and alertness, in cerebration, in drive, but not particularly interested in the direction which these things take. His inclination is to dissect history and civilization, and to reduce it to a list of functions, which he does not connect together very firmly. He is adept at passing from one matter to the next, leaving the reader flat. He raises interest and excitement, only to provide an anti-climax. The nearest he gets to the great synthesis of his life's work is this: 'Civilization is the unfinished, and perhaps never-to-be-finished, product of some great evolutionary force which permeates all nature. Second, the action of this force is swayed by the great factors, namely, biological inheritance, physical environment, and cultural endowment. Third, these three constantly rest upon one another, and a knowledge of their combined influence is a prerequisite to a full understanding of history. When all three factors are favourable, civilization makes rapid progress; when all are unfavourable retrogression is the rule.' If Huntington can be naïve enough to write this, your reviewer can equally naïvely ask how he arrives at the idea in the first sentence and how, if there is such a force, the things he mentions can sway it.

However, if Huntington does not rise to a noble synthesis, he succeeds in making a great amount of analysis: his analyses are original, and ingenious, have occupied a lifetime, and deserve to be widely read and discussed. In a review it is possible to sort out, from such a tremendous list of subjects, few for mention and fewer for criticism; but one must specially list: an analysis of Puritan descent in U.S.A., leading Huntington to the conclusion that the results of selection by migration may persist with strength for centuries; a comparison of the cultural achievements of Iceland and Newfoundland, showing how in two climatically adverse but similar countries there may be great differences in human temperament and intellectual capacity which are inherited; a further statement of the theory of human kiths, with illustrations from the Parsis, the Jews, the Moabites, the Puritans, the people of Adare in western Ireland, the

Mongols, the Manchus and the Junkers; a discussion of the effects of nomadism on character. All these are from the first third of the book.

One of Huntington's chief concerns is with the measurement of civilization, and his methodology is original and ingenious. Some of his maps have been published in previous works, which has led him into glossing over the data on which they are based and in certain cases omitting any explanation of the units on which the plots are built. But the general effect of his galaxy of examples is great, and much stimulating to thought. For instance, in Chapter 12, after looking at maps of the U.S.A. showing crowding of dwellings, net (white) reproductive rate, homicides (of whites), economic and social prosperity, distribution of urban population, standardized death-rates at different ages and from different causes, 'climatic efficiency' on the basis of factory work and on the basis of deaths, we get the impression of a rigid basic pattern. Huntington's thesis is that the only factor capable of producing this pattern, which shows the maximum of 'civilization' in a west-coast belt and in another from Chicago to New York, is 'climate acting upon the health and vigor of the people'.

It is apt here to comment that in his treatment of human heredity Huntington shows a generally Lamarckist point of view.

The second half and more of the book is devoted to a discussion of climate and civilization. Much of this is summarized from his previous books, such as *Principles of human geography*. From his discussion certain very interesting points stand out. Is there an annual cycle of reproduction in man; or rather, can the fact that there are more conceptions at some seasons than at others constitute the existence of a true reproductive cycle? What factors determine the increase in human conceptions in summer or autumn? How far are the cultural and political differences between South and North in U.S.A. attributable in the long run to climate? Is there a correlation between the level of religious thought and the equability of climate? What *is* the most equable climate? Why should the storminess of climate affect human mental and physical vigour, as it appears to do? Huntington asks these questions and demonstrates them, and suggests partial solutions.

Three chapters deal with cycles; in these Huntington has been helped by Edward R. Dewey, Director of the Foundation for the Study of Cycles. Huntington appears to accept the existence of some of these cycles uncritically, and to a somewhat suspicious (and non-statistical) eye some of the graphs he produces seem like special pleading. But first approximations are truly valuable, and never harm those bold enough to state them; and the cycle part of this book seems to be the most valuable part for the ecologist. The cycles mentioned include (with what follow, or are alleged to follow, them):

2 years: fruit crops.

3·4 years (41 months): business activity and atmospheric electricity.

3⅔ years: Nile floods and atmospheric pressure.

4 years: animal population.

7½ years: tree growth, lake deposits and atmospheric pressure.

8 years: wheat prices.

9·2 years: prices.

9⅔ years: prices, animal population, tree growth and atmospheric ozone.

11·2 years: sunspots.

22·3 years: sunspots.

35 years: European weather.

45 years: weather.

54 years: commodity prices.

68 years: commodity prices and Nile floods.

90 years: weather.

170 years: drought and civil war.

510 years: drought.

Mainsprings of civilization may leave the reader puzzled, even irritated, but if fair-minded he will realize that his irritation can be directed against the state of our knowledge. As an indication of how small, scattered and muddled our knowledge of our own environment is the book is splendid, and it will stimulate a desire to research wherever it is read.

<div style="text-align: right">JAMES FISHER</div>

A RUSSIAN TEXT-BOOK

D. N. Kashkarov (1944). [*Fundamentals of animal ecology*.] (In Russian.) 2nd ed. 383 pp., 163 text-figures. Leningrad. Price 20.75 roubles.

Although stated to be a second edition of a University text-book on animal ecology, it is actually the third. The first appeared in 1933 under the title *Environment and Biocoenosis (Foundations of Synecology)* and the second in 1938 under the present title (see reviews in this *Journal*, 2: 125–6; 8: 171–2). The present edition had been thoroughly revised by the author before the outbreak of the war but he did not live to see it through the press, having died in 1941 (see obituary in this *Journal*, 14: 52–3).

The three editions of the book show clearly that Kashkarov was not a man of set ideas. The title of the first edition implied an emphasis on synecology, and the contents reflected more the influence of American-ecological school than original work and conceptions. In the second edition, Russian ecological data and ideas loomed large, and in the latest edition a balance has been established between material from Russian sources and the foreign ones, though a neglect of European continental work is still apparent.

The book, in its latest edition, is divided into nine chapters. In the first, the subject and problems of ecology and its methods are discussed, and a brief outline of the history of ecology is given. The second chapter deals with factors of the environment, the climatic ones, including ecoclimate and microclimate, receiving very adequate treatment. Life zones and their subdivisions form the subject of the third chapter, while the fourth deals with the problem of adaptations and life forms. Chapter V, on acclimatization and ecology of domestic animals, contains valuable data on Russian work in applied ecology. The sixth chapter deals with the problem of biocoenoses, including their structure, dynamics and succession. This leads to Chapter VII, 'Evolution and ecology', in which the ecological and evolutionary importance of phenotypic variation is stressed, in accordance with the latest trends in Soviet genetics. Chapter VIII, on quantitative survey methods in ecology, will be of interest

to Western ecologists as it is mainly based on Russian data, but work done elsewhere is presented very inadequately. The last, ninth, chapter deals with the ecology of desert as an illustration of interrelations between environment, organisms and their groupings. Ten pages of bibliography of Russian ecological works contain a mass of references little known abroad, but the bibliography in other languages is less complete and almost entirely restricted to American and English works.

A thoroughly dynamic and critical approach to all problems, coupled with a praiseworthy moderation in the use of concepts and definitions, so well beloved by some modern ecologists, make Kashkarov's book outstanding amongst others. The wealth of data extracted from recent Russian ecological work make the book particularly valuable for ecologists of other nations, but how many of them will be able to read it? The need for a wide interchange of information and of ideas with Soviet scientists is at present stressed on every occasion, but practical steps towards achieving this aim are scarce. One such step would be to arrange for the translation and publication in this country of Russian scientific books that deserve to be known abroad, and Kashkarov's book certainly belongs to this category.

<div align="right">B. P. UVAROV</div>

POPULATION THEORIES

Umberto d'Ancona (1942). *La Lotta per l'Esistenza*. 357 pp. 54 text-figures. Giulio Einaudi, Torino, Italy. (Bibliotheca di Cultura Scientifica, No. 9.)

This book by the Director of the Institute of Zoology and Comparative Anatomy in the University of Padua is an excellent survey of those mathematical theories which are associated principally with the names of Lotka and Volterra. As is natural and understandable in the case of a treatise written in Italian, the greater part of the book is devoted to the mathematics of the interrelations between populations which were developed so brilliantly by Volterra in the years before his death. It will be of great value to biologists in England and America to have this convenient summary of his work at hand within the covers of a single volume. One chapter is given to 'the equations of Lotka', and, if a criticism has to be offered, this portion of the book might perhaps have been expanded further and a fuller account given of the fundamental contributions which have been made by Lotka to demography and population mathematics. But this is a

small point, and it will hardly affect American or English readers who are familiar with *The Elements of Physical Biology*.

If Prof. d'Ancona had set out merely to summarize the mathematical theories of Volterra, he would have performed a valuable service; but he has done more than this. In addition he has described briefly the contributions made by Ross, Martini and Lotka to the mathematics of epidemiology, and the more recent work in this field by Kermack and McKendrick. He deals with the problems of the interrelations between host and parasite, and the work of Thompson and of Bailey and Nicholson in this connexion. Later, in regard to the struggle for existence and evolution, he touches on the mathematical developments initiated by Fisher, Haldane and Wright, and in a further chapter also to the extensions of Volterra's theory which have been made by Kostitzin. It is evident from this very brief and incomplete summary of the contents of this book that a wide field has been covered by the author, and that the reader will find it, apart from its other great merits, a most valuable book of reference. An English translation would enable it to be read more widely, and an index (there is none in the Italian edition) would be of great assistance. There is a bibliography of some 13 pages, though on a cursory glance it appears to be somewhat incomplete: thus the names of neither Fisher nor Haldane, although referred to in the text, are to be found in it.

Finally, it is to be observed that the chapters on the verifications of the mathematical theory, 'Verifiche tratte dall'osservazione naturale' and 'Verifiche sperimentali', run to 14 and 19 pages respectively out of a total of 341 pages of text. It is a melancholy thought that the contributions made up to 1939 by experimental science to the confirmation or modification of the mathematics can be condensed into such a small space. It is to be hoped that, with a lessening of the burden of applied work, more biologists will turn their attention to this field, in which, given adequate technical facilities and imaginative insight into the design of such experiments, they surely will not fail to obtain interesting and important results. The work will, however, be difficult and lengthy; but until this side of biology is developed much further, the gap which is at present so unsatisfactorily bridged will remain between the mathematician and the experimentalist. It is an amusing, and a far from unprofitable speculation to consider the way in which theoretical physics might have developed if only an occasional experiment had been done.

<div align="right">P. H. LESLIE</div>

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W.1, or through a bookseller, price 3s. 6d. per annum post free (in two sets, May and November).

Abstracting has been done voluntarily by H. F. Barnes, D. Chitty, C. Elton, R. B. Freeman, B. M. Hobby, E. M. O. Laurie, Barrington Moore, E. Nelmes, F. T. K. Pentelow, H. N. Southern and H. V. Thompson.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(a) MARINE AND BRACKISH

Cooke, R. (1946). 'Black terns breeding in Sussex.' Brit. Birds, 39: 71–2.

The interesting fact is recorded that *Chlidonias niger*, extinct as a breeding species for many years, occupied and bred in an area near Winchelsea, while it was flooded during the war as a precaution against invasion. The provision of a habitat was evidently a key factor here, though it is curious that other places, e.g. East Anglia, have not been used.

Bloomer, H. H. (1945). 'The distribution of *Crepidula fornicata* L.' J. Conch. 22: 147.

Records occurrence of this molluscan enemy of oysters in Studland and Swanage bays, and its absence farther west from Durlston Bay to Lulworth Cove.

Wells, G. P. (1945). 'The mode of life of *Arenicola marina* L.' J. Mar. Biol. Ass. U.K. 26: 170–207.

Field observations showed the typical burrow not to be an open U, but to have one limb (the 'head shaft') filled by a column of sand which is 'worked' by the worm. Laboratory studies indicated that the working is done by the irrigation current, upward movements of the worm, and feeding from the base of the head shaft.

Atkins, W. R. G. (1945). 'Conditions for the vernal increase in the phytoplankton and a supposed lag in the process.' Nature, Lond. 156: 599.

Light alone is claimed to be the limiting factor for the full development of the phytoplankton; there being no necessity for an 'unrecognised' factor. The small number of plankton cells present after the winter makes an apparent lag a mathematical necessity.

(b) Fresh water

Underdown, H. C. B. (1945). 'Birds of the riverside: VIII. The sedge warbler. [IX. The reed warbler.]' Salm. Trout Mag. (Lond.), No. 115: 239–41.

A popular account of the habits and life histories of *Acrocephalus schoenobaenus* and *A. scirpaceus*.

Underdown, H. C. B. (1946). 'Birds of the riverside: X. The common redshank. [XI. The common sandpiper.]' Salm. Trout Mag. (Lond.), No. 116: 44–7.

A non-technical account of the distribution, habits and food of *Tringa totanus* and *T. hypoleucos*.

Popham, E. J. (1945). 'Some observations on the distribution of *Velia currens* (Hemiptera).' Entomologist, 78: 145–8.

A study of any stream colonized by *Velia currens* shows that this species is not scattered evenly over its surface, but is found in greatest numbers near the banks and on other slowly moving sections of the stream. Its distribution is the result of the interaction of several factors. Its positive phototactic movements combined with rapid powers of light adaptation and its relative speeds in dim and bright light as well as its reactions to wind and the roughness and speed of the water, all play their part in causing the species to congregate in large numbers under the banks and other sheltered places, or where the speed of the water and wind do not exceed 0·21 and 2·16 m.p.h. respectively.

Christophers, S. R. (1945). 'Structure of the *Culex* egg and egg-raft in relation to function (Diptera).' Trans. R. Ent. Soc. Lond. 95: 25–34.

The egg-rafts of species of *Culex* examined show constant specific characters. The raft of *C. molestus* is strikingly smaller than that of *C. pipiens*. *Theobaldia annulata* also produces a raft.

Classey, E. W. (1944). 'The mosquitoes of the Hants.-Surrey border (Blackwater Valley region).' Proc. R. Ent. Soc. Lond. A, 19: 109–14.

In this survey three collecting methods were used: (1) collecting larvae, (2) collecting resting adults and (3) exposing various parts of the body and collecting the females which come to bite. The first method was by far the most remunerative, the only species which were not taken by this method being *Culex molestus* and *Taeniorhynchus richiardii*, both of which were taken by the third method. Ecological details of habitats are given.

Gibson, N. H. E. (1945). 'On the mating swarms of certain Chironomidae (Diptera).' Trans. R. Ent. Soc. Lond. 95: 263–94.

Swarming habits of Chironomids common about sewage works are compared with recorded facts about Culicines. *Spaniotoma minima* and *Metriocnemus* spp. are diurnal swarmers, *Chironomus dorsalis* is crepuscular.

Brown, E. S. (1945). 'The nymphal stage of *Capnia atra* Morton (Plecopt., Capniidae), with a description of certain distinguishing features.' Proc. R. Ent. Soc. Lond. A, 20: 50–3.

Includes details of habitat and emergence dates in captivity of this stonefly.

Lloyd, L. C. (1945). 'Shropshire dragonflies.' Northw. Nat. 20: 68–70.

Distributional records for 20 species.

Allen, P. B. M. (1945). '*Gomphus vulgatissimus* L. in Montgomeryshire.' Northw. Nat. 20: 70.

This local dragonfly observed near Newtown.

Wattison, J. T. (1945). '*Gomphus vulgatissimus* L. in Shropshire.' Northw. Nat. 20: 70.

Male of this local dragonfly captured near Bridgnorth on 8 May 1941.

Černosvitov, L. (1945). 'Oligochaeta from Windermere and the Lake District.' Proc. Zool. Soc. Lond. 114: 523–48.

Records of 17 species with some ecological notes and detailed descriptions of species which had previously been confused. 13 terrestrial Oligochaeta are also recorded and discussed in some detail.

<div align="center">(c) LAND</div>

Lloyd, L. C. (1945). 'Yellow-necked mouse in Shropshire.' Northw. Nat. 20: 64.

Records the trapping of several specimens of *Apodemus flavicollis wintoni* at Clunton in June 1945. This local species has been reported from three other districts in Shropshire and may have been overlooked elsewhere.

Lloyd, L. C. (1945). 'The evening flight of the pipistrelle bat.' Trans. Caradoc Fld Cl. 11: 259–64.

A series of observations on time of emergence of *Pipistrellus pipistrellus* during the summer months. Very close correlation between sunset and time of emergence is shown; the average time being 27·5 min. after sunset (standard deviation 7 min., range 1–43 min.). No correlation could be found with pressure, temperature or cloud cover. There were indications of a moderate degree of correlation between a high relative humidity and a later emergence of the bats.

Lancum, F. H. (1945–6). 'Wild animals and agriculture.' J. Minist. Agric. 52: 228–31, 276–8, 331–4, 371–3, 422–4, 464–7, 520–2.

Popular accounts of the rat, hare, weasel family, the water-vole and others, shrews and mole.

Ryves, B. H. & Quick, H. M. (1946). 'A survey of the status of birds breeding in Cornwall and Scilly since 1906.' Brit. Birds, 39: 3–11, 34–43.

A survey under species headings of increase, decrease and stability since the last major work upon this area.

Griffiths, W. & Wilson, W. (1945). The birds of North Wirral.' Northw. Nat. 20: 37–47.

This continued annotated list deals with 65 species and is itself to be continued.

Boyd, A. W. (1945). 'Columbaria.' Northw. Nat. 20: 67.

Disused dove-cotes in Cheshire are used as nesting sites by barn-owls (*Tyto alba*), and where they have fallen into disrepair, owl populations have declined. A newly built cote quickly attracted a nesting pair.

Ellison, N. F. (1945). 'Notes on the nest and site of a willow tit, *Parus atricapillus kleinschmidti*, Hellm.' Northw. Nat. 20: 67–8.

Describes nest in a rotten stump of silver birch. The lining materials included feathers from several different species.

Glasman, M. C. (1945). 'Notes on the swallow.' Peregrine, 1 (3): 9–11.

Includes dates of arrival of *Hirundo rustica* and full data for three broods, and ringing statistics.

Townsend, C. C. (1945). 'The Coleopterous and Heteropterous fauna of a dry carbon tip.' Ent. Mon. Mag. 81: 166–8.

Account of fauna of dump from the tar gas plant of the gasworks at Cheltenham. By far the majority of the species were Carabidae.

Lloyd, R. W. (1945). 'Inhabitants of the jackdaws' nests.' Ent. Mon. Mag. 81: 249.

Larvae of the beetle *Attagenus pellio*, an adult beetle *Niptus hololeucus* and several spiders (*Stearodea bipunctata*) in nests of *Corvus monedula*.

Freeman, R. B. (1945). 'Coleoptera from nests of the robin.' Ent. Mon. Mag. 81: 216.

Five nests of *Erithacus rubecula* taken in Wytham Wood, Berkshire, were examined. One contained no beetles, but the others contained 33 specimens belonging to 17 species, several of which are scarce or local.

Mansbridge, W. (1944). 'The Lepidoptera of an alder carr.' Rep. Lanc. Chesh. Ent. Soc. 64–7: 41–2.

About 50 to 80 years ago at various points on the sandhills of the Lancashire coast alders were planted where there were soft muddy depressions. These vary in extent from one to three or four acres. A list of 41 Lepidoptera from these and similar places in other parts of Lancashire and Cheshire is given.

Wilson, G. Fox (1945). 'Insect pests of *Cotoneaster horizontalis*.' J. R. Hort. Soc. 70: 271–5.

Contains notes on the appearance, bionomics and control of two aphids, two coccids and five Lepidoptera, all indigenous, that feed on *Cotoneaster horizontalis*, introduced from China. *Eriosoma lanigerum* often attacks wall-trained plants, but apparently belongs to a different biological race from that found on apple. Its distribution in England and that of *Lecanium corni, Eurhodope suavella* and *Scythropia crataegella* are shown on a map. The range of *S. crataegella* on *Cotoneaster* is increasing.

Williams, C. B. (1946). 'Climate and insect life.' Nature, Lond. 157: 214–15.

Commenting upon the importance of correlating changes in numbers of insects with meteorological conditions, it is suggested that this may best be achieved by field experiments; the complex data being analysed statistically. Experiments at Rothamsted have enabled the abundance of insects to be forecast from the weather conditions of the previous months; the determining factors were rainfall, in the summer, and temperature, in the winter.

Perkins, R. C. L. (1945). 'The Aculeate Hymenoptera of a small area of Dartmoor near Lydford, Devon.' Ent. Mon. Mag. 81: 145–53.

95 species of bees, 26 of sphecoid wasps and 24 of vespoid wasps (including two Chrysids) were collected. The total number of species is almost the same as for the whole Irish fauna in these groups, and excluding those from sandy and well-wooded districts there is a striking similarity between the two faunas. A large number are local, very local, rare or very rare. The similarity of the faunas is largely due to their consisting of species which are particularly hardy and can exist under weather conditions which are impossible for many of our species.

O'Rourke, F. J. (1945). 'A further extension of the range of *Myrmica schenki*, Emery.' Ent. Rec. 57: 85–6.

New localities recorded for this rare ant are in West Cork and Co. Galway. The only other known stations are Co. Dublin, Co. Carlow and Glamorgan.

Hinton, H. E. (1944). 'Some general remarks on sub-social beetles with notes on the biology of the Staphylinid, *Platystethus arenarius* (Fourcroy).' Proc. R. Ent. Soc. Lond. A, 19: 115–28.

The occurrence of subsocial habits in beetles is briefly reviewed. The female of *P. arenarius* constructs a brood chamber in cow dung. She remains in the brood chamber throughout the incubation of the eggs and usually during the first few days of the life of the young larvae. During this period she will attack other insects entering the brood chamber. She also protects her young against fungi. Both larvae and adults of *P. arenarius* will feed exclusively on cow dung. Larvae fed exclusively on cow dung will produce normal adults.

Massee, A. M. (1945). 'Abundance of *Labidostomis tridentata* L. (Col., Chrysomelidae) in Kent.' Ent. Mon. Mag. 81: 164–5.

This beetle occurred in great profusion on young seedling birch trees at East Malling, Kent, in May. It is very active on warm sunny days and flies readily from early morning until dusk, but is unable to travel long distances. It has been found sparingly in this district since 1921.

Duffy, E. A. J. (1945). 'The Coleopterous fauna of the Hants.-Surrey border.' Ent. Mon. Mag. 81: 169–79.

Includes sketch-map showing geological formations and numerous notes on habitats.

Day, F. H. (1945). 'The wall butterfly, *Pararge megaera* L. (Lep., Satyridae) in Northern England.' Ent. Mon. Mag. 81: 272.

Around Carlisle the wall butterfly has been common for the past 50 years. In the east of Cumberland and in the Lake District it appears to be comparatively scarce.

Wiltshire, E. P. (1945). 'Studies in the geography of Lepidoptera. III: The zoogeographical classification of West Palearctic species.' Entomologist, 78: 113–16, 131–6.

Pleas for an eco-faunistic classification running parallel with geographical classification.

Bedwell, E. C. (1945). 'The county distribution of the British Hemiptera-Heteroptera.' Ent. Mon. Mag. 81: 253–73.

Chart of all known English and Welsh records, by counties. Scottish and Irish records are given without further subdivision. No references to sources or literature.

Dicker, G. H. L. (1945). 'Notes on some British Coreids (Hemiptera-Heteroptera).' Ent. Mon. Mag. 81: 278–9.

Gives habitat notes.

Shaw, H. K. Airy (1945). 'Additions to the list of Bedfordshire Hemiptera-Heteroptera.' Ent. Mon. Mag. 81: 183–5.

Gives precise habitat notes.

Wright, A. E. (1945). 'Diptera of North Lancashire and South Westmorland.' Northw. Nat. 20: 47–9.

A preliminary list of 42 species belonging to nine families, indicating their distribution and abundance.

Goffe, E. R. (1945). '*Volucella zonaria* (Poda, 1761) (Dipt., Syrphidae) in Britain.' Ent. Mon. Mag. 81: 159–62.

There are now six authentic British specimens in collections, three reputed British but without data of capture, and one taken off the Kentish coast. Published records, with one exception, allude to the coastal counties of Kent, Sussex, Hampshire and Dorset and suggest that its introduction to Britain may have been by migration from France. Its occurrence at Folkestone for at least three consecutive seasons suggests that it has bred in that area; and captures at Weymouth, Dorchester and Bristol suggest a second establishment and extension covering at least four seasons. These cases, and the fact that it appears to have been noticed here over a long period of years, suggest equally strongly that it is established in south and south-eastern England. Key given.

Fraser, F. C. (1945). '*Volucella zonaria* (Poda) (Dipt., Syrphidae) in Bournemouth.' Ent. Mon. Mag. 81: 237–8.

Eight specimens seen or captured at Bournemouth, Hants. Apparently one seen sitting at the mouth of a wasps' nest (*Vespula vulgaris*) in which the larvae are scavengers.

Roebuck, A., Baker, F. T. & White, J. H. (1945). 'Observations on the biology and experiments on control of the mangold fly (*Pegomyia betae* Curtis) on sugar-beet.' Ann. Appl. Biol. 32: 164–70.

Ecological and phenological aspects in central Nottinghamshire. Some pupae of the second generation fail to emerge in the late summer but emerge rather earlier in the following spring than pupae of the third generation. Such retarded flies are less fertile than usual.

Wilson, G. Fox (1945). 'Small-scale carrot fly control.' J. Minist. Agric. 52: 219–23.

Includes notes on the habits of the *Psila rosae*.

Wright, A. E. (1945). 'Syrphidae from N. Lancashire and S. Westmorland in 1944.' Northw. Nat. 20: 71–2.

Includes two additions to previous lists of hover flies.

Thompson, J. L. Cloudsley- (1945). 'Behaviour of the common centipede *Lithobius forficatus*.' Nature, Lond. 156: 537–8.

Experiments showed negative phototaxy and positive thigmotaxy, also the importance of the antennae in foraging. Some habits are described.

Collinge, W. E. (1945). 'Notes on the terrestrial Isopoda (woodlice). No. XII.' Northw. Nat. 20: 5–10.

Contains notes on duration of life of *Armadillidium vulgare* and *Oniscus asellus* in captivity; a list of 13 species from the littoral zone of Ireland, some of which have hitherto been regarded as inland species, and the number of species recorded from each of 27 counties from which further records are desired; a list of six species that are likely to occur in Yorkshire, but have not been recorded there, and a request for information from that county; an instance of oviposition by *A. vulgare* directly on to the ground without the medium of a brood pouch; and the bionomics in captivity and habits, reactions to temperature, habitat, and colour variations of *A. vulgare*.

Stelfox, A. W. (1945). 'A large race of *Cepaea nemoralis* L. (and other Mollusca) at high altitudes in the Galtee mountains, Co. Tipperary south.' J. Conch. 22: 168.

Records a colony of reddish, often white-lipped, large forms from 1800–2000 ft. and probably higher. The rock is old red sandstone, and not Carboniferous limestone as is usual with the large races. The fresh-water limpet *Ancylastrum fluviatile* is recorded abundantly on wet rock surfaces.

(*d*) SMALL ISLANDS

Wagstaffe, R. (1945). 'Natterer's bat. A new Manx mammal.' Peregrine, 1 (3): 1.

Myotis nattereri is the first land mammal to be added to the list of Manx species since 1885. The only other bats recognised as occurring in the island are *Pipistrellus pipistrellus* and the long-eared bat, *Plecotus auritus*.

Ellison, N. F. (1945). 'Short-tailed vole on Hilbre Island, Cheshire.' Northw. Nat. 20: 63–4.

A well-established and flourishing colony of *Microtus agrestis* present on cliff-tops in April 1945, but not in 1939–41, may have originated from individuals introduced with hay carted from the mainland, access to which at low tide would be difficult for small mammals. It is probably correlated with the unusual appearance of a pair of kestrels that were present for several weeks.

Barlee, J. & Ruttledge, R. F. (1945). 'Notes on the present status of birds on Clare Island.' Irish Nat. J. 8: 311–13.

Notes on a decrease in land birds generally since the last survey (1911). Between 180 and 280 pairs of fulmar (*Fulmarus glacialis*) were present on the cliffs on 25–27 April ? 1945.

Williamson, K. (1945). 'The Manx shearwater in the Faeroes.' Peregrine, 1 (3): 2–4.

Puffinus puffinus breeds in many places in the Faeroes, but is now hunted only on Koltur, Nlósoy and Tröllhövdi. About 250 are taken annually on Tröllhövdi and about 200 on Koltur.

Crellin, R. & Crellin, G. (1945). 'Nesting of the long-tailed tit.' Peregrine, 1 (3): 24–5.

Parus caudatus has been seen in the Isle of Man on several occasions during the past few years. It was first recorded as nesting in the island in 1942. Details of three nests are given.

Corbet, A. S. (1945). 'The Lepidoptera of St Kilda.' Entomologist, 78: 166–8.

Thirty species are listed. The small heath butterfly (*Coenonympha pamphilus*) formerly recorded from the island has not been seen by later collectors and it is very doubtful if it still occurs there. *Apamea monoglypha* and *Orthosia incerta* were represented by dark forms. The commonest moth recorded by Hewitt (1907) was *Sterrha rusticata*, a species otherwise confined to southern England.

Wilks, R. L. (1945). 'Some notes on the Macro-Lepidoptera of Islay.' Entomologist, 78: 161–5.

Collector's notes for 1941, chiefly dates of occurrence and estimates of abundance.

Harrison, J. W. Heslop (1945). '*Apatele psi* L. in the Outer Hebrides.' Entomologist, 78: 189–90.

This moth may be a survival from an old woodland fauna in the Outer Hebrides.

Hedges, A. V. & Cowin, W. S. (1945). 'Notes on Manx Lepidoptera.' Peregrine, 1 (3): 6–7.

List of moths additional to the Isle of Man.

Wright, A. E. (1945). 'A Manx record of the Scotch Argus butterfly.' Peregrine, 1 (3): 8–9.

Erebia aethiops is common in Scotland, but Westmorland is the most southerly of its present British habitats, although it formerly occurred at Grassington in Yorkshire and Grange-over-Sands. The record here cited appears to have been overlooked; it was published in 1869 and states several were taken in July and August on the hills in the direction of Laxey and Onchan.

Cowin, W. S. (1945). 'The spread of the orange-tip butterfly in the Isle of Man.' Peregrine, 1 (3): 22–4.

Euchloe cardamines has long been regarded as a rarity in the Isle of Man. In 1937 a male was seen, in 1940 four males, in 1941 there was a remarkable increase, one observer reporting fifty on a single day. Strong colonies in many places have since been reported.

Bailey, J. H. & Britten, H. (1945). The Coleoptera of the Isle of Man.' Northw. Nat. 20: 51–62.

This list adds 116 species (Dascillidae-Curculionidae) to a previous one and is to be continued.

Paton, C. I. (1945). 'Harvestmen.' Peregrine, 1 (3): 4–5.

Six species: *Liobunum rotundum, Phalangium opilio, Mitopus morio, Oligolophus tridens, O. agrestis* and *Nemastoma lugubre* have been taken in the Isle of Man.

Paton, C. I. (1945). 'Woodlice.' Peregrine, 1 (3): 5.

Adds *Trichoniscus roseus, Haplophthalmus mengii, H. danicus* and *Porcellio spinicornis* to the list of Isle of Man species.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Thorpe, W. H. (1945). 'The evolutionary significance of habitat selection.' J. Anim. Ecol. 14: 67–70.

From recently investigated cases of habitat selection it is suggested that geographical, topographical, and ecological isolation are best regarded as different scales of spatial isolation. Recent developments in animal learning do not support Mayr's claim that geographical isolation *always* precedes other kinds of isolation. Probably it works together with habitat or locality preference, and in exceptional cases habitat preference may alone initiate the process of separation, by starting differences in habit maintained at first by 'tradition'.

Bullough, W. S. (1945). 'Endocrinal aspects of bird behaviour.' Biol. Rev. 20: 89–99.

Species formation may arise through the effective isolation of groups of birds because of changes in the endocrine glands induced by changes in behaviour.

Association of Applied Biologists. (1945). Discussion on nomenclature problems of the applied biologists.' Ann. Appl. Biol. 32: 181–8.

Includes 'Reasons for name-change and the stability of names' by **J. Ramsbottom**, 'How shall we name insects?' by **A. Roebuck** and 'Synonymy of Aphididae' by **I. Thomas**.

Donisthorpe, H. St J. K. & Morley, D. B. W. (1945). 'A list of scientific terms used in myrmecology.' Proc. R. Ent. Soc. Lond. A, 20: 43–9.

Collin, J. E. (1945). 'British Micropezidae (Diptera).' Ent. Rec. 57:115–19.

Keys and distribution. Nothing is known of the life history of any British species, but there are records of exotic species breeding in decaying vegetable matter and rotten wood.

3. PARASITES

Hickin, N. E. & Robins, E. L. D. (1945). 'Psocids infesting puppies.' Ent. Mon. Mag. 81: 214.

Puppies infested by *Trogium pulsatorium*, a very common household book-louse.

Harvey, J. H. (1944). 'Observations on the parasites of the cabbage butterflies.' Lond. Nat. 1943: 12–19.

Of 233 *Pieris brassicae* collected in Flintshire in 1942, 19·3 % were parasitized by *Pteromalus puparum* and 55·4 % by *Apanteles glomeratus*. Larvae that pupated after the end of October were not attacked. Emergence of *Pteromalus puparum*, which also attacked *Pieris rapae* took place in June, when pupating host larvae were available, and 300 emerged from 14 host pupae. Larvae of *Pieris* containing *Apanteles* were able to climb as high as unparasitized ones before pupating. Nearly all the *Apanteles* under observation were destroyed by *Hemiteles fulvipes*, which attacked them in autumn and again in April–May, *Dibrachys cavus*, and *Tetrastichus rapo*. Many pupae of *Apanteles* and *Pieris* were destroyed in winter by blue tits (*Parus caeruleus*) and possibly spiders. Tentative suggestions for controlling *Pieris* by rearing and liberating *Pteromalus* and unparasitized *Apanteles* are made.

Butler, C. G. (1945). 'The incidence and distribution of some diseases of the adult honeybee (*Apis mellifera* L.) in England and Wales'. Ann. Appl. Biol. 32: 344–51.

Surveys of acarine disease, *Nosema* disease, *Amoeba* disease and bee paralysis.

Wilkinson, D. S. (1945). 'Description of Palearctic species of *Apanteles* (Hymen., Braconidae).' Trans. R. Ent. Soc. Lond. 95: 35–226.

Critical descriptions of this parasite genus illustrated with numerous figures, and many distributional records for Britain, with notes on biology where known.

Blair, K. G. (1945). 'Notes on the economy of the rose-galls formed by *Rhodites* (Hymenoptera, Cynipidae).' Proc. R. Ent. Soc. Lond. A, 20: 26–31.

Notes on the inquilines, parasites and gall-formers of the Bedeguar gall, smooth pea-gall and spiked pea-gall.

4. FOOD AND FOOD HABITS

Lack, D. (1945). 'The ecology of closely related species with special reference to cormorant (*Phalacrocorax carbo*) and shag (*P. aristotelis*).' J. Anim. Ecol. 14: 12–16.

These two species occur together in the same regions but do not compete to any great extent either for nesting sites or for food. They are thus not an exception to Gause's thesis that animals with similar ecology cannot live in the same area. Ecological isolation occurs in other groups of animals with closely related species that occupy the same range.

Colquhoun, M. K. (1945). 'The wood pigeon.' Scot. J. Agric. 25: 178–82.

Availability of food, food and feeding habits, food preference, movements and breeding of *Columba palumbus*.

Frost, W. E. (1945). 'River Liffey survey—VI. Discussion on the results obtained from investigations on the food and growth of brown trout (*Salmo trutta* L.) in alkaline and acid waters.' Proc. Roy. Irish Acad. 50 (B) 19: 321–42.

Small slow-growing trout are usually found in acid and larger quick-growing trout in alkaline waters. There is an ample food supply at both alkaline and acid stations examined, though qualitatively it is in favour of the fish at the alkaline station. Size is determined during the first year when the rate of growth is more rapid for trout in alkaline than acid waters. Subsequent growth is much the same for both. Analysis of bones gives no indication of calcium deficiency, but the volume of water required to provide the necessary calcium is greater for fish in acid waters. Growth may be affected by the acid character of the water. There is no evidence that the spawning grounds are better in the acid waters.

Hodgson, S. B. (1945). '*Zygaena lonicerae* pupae eaten by birds.' Entomologist, 78: 176.

Records extraction of pupae of this moth from cocoons.

Richards, O. W. (1944). 'Observations on Aculeate Hymenoptera.' Proc. R. Ent. Soc. Lond. A, 19: 133–6.

Notes on the habits and prey of *Trypoxylon figulus, Crossocerus anxius, Entomognathus brevis, Ectemnias dives, Calicurgus hyalinatus, Pompilus trivialis, Mimesa shuckardi, Cerceris rybyensis*; two generations of *Nomada fucata* and the host of *N. flavopicta*; and hosts of various *Sphecodes* spp.

Staniland, L. N. (1945). 'The occurrence of *Anguillulina dipsaci* (Kühn) on weed hosts, including new host records in fields of oats affected by "tulip-root".' Ann. Appl. Biol. 32: 171–3.

Cleavers, common chickweed, mouse-ear chickweed and sandwort as hosts of this nematode. Transferences from chickweed to oats, from oats back to chickweed and from cleavers and sandwort to oats.

5. POPULATION STUDIES

Parrinder, E. R. & Parrinder, E. D. (1945). 'Some observations on stonechats in North Cornwall.' Brit. Birds, 38: 362–9.

A study throughout the breeding season of fifteen pairs of *Saxicola torquata* distributed along cliff marginal common land with gorse and heather. Territories varied in size from $\frac{3}{4}$ to $2\frac{1}{2}$ acres and composed altogether some 30 % of the area available. Breeding started in late March, and of the fifteen pairs, seven raised a second brood, and five a third brood. Pairs that ceased breeding apparently moved out of the area. Fledging success was very high (over 90 % of the eggs laid). The whole picture suggests that the species here may have been recovering from a low level of numbers.

Williamson, K. & Cowin, W. S. (1945). 'The nature of the rookery.' Peregrine, 1 (3): 12–19.

The rook (*Corvus frugilegus*) population of the Isle of Man has remained remarkably stable throughout the survey period, 1938–45, recent decreases being due to persecution rather than natural causes. Its upper limit is probably of the order of 6500 breeding pairs. Variation in total nest counts had a striking correlation with the late winter sunshine records. The rookery is an unstable unit, a settlement of convenience rather than of habit or tradition, and the degree of its occupation is determined by the availability of food supplies, which are in turn dependent on the type of season and the agricultural treatment of the land. The insular population, though fairly static in number under natural conditions, is therefore exceedingly fluid, the varying ecological conditions keeping a large number of rooks continually on the move from place to place.

Russell, E. S. (1946). 'Fishery research and the overfishing problem.' S. East. Nat. 50: 37–50.

A general exposition of the sea fishery problem, stressing the effect of overfishing, particularly in the North Sea (reviewed in J. Anim. Ecol. (1943) 12:59). As a result of reduced fishing during the war years, a trawler fleet with only 40 % of its pre-war strength caught as much hake in 1942–4 as did the entire fleet in 1936–8. The fish were also of much larger size.

Hickling, C. F. (1945). 'Marking fish with the electric tattooing needle.' J. Mar. Biol. Ass. U.K. 26: 166–9.

Plaice and sole were much easier to mark than rays, and no apparent injury resulted. Marks on the flatfish were faint but legible after seven weeks, those on the rays illegible after four days.

Hickling, C. F. (1945). 'The seasonal cycle in the Cornish Pilchard, *Sardina pilchardus* Walbaum.' J. Mar. Biol. Ass. U.K. 26: 115–38.

Seasonal variations in mean weight and fat content of fish are correlated. Examination of the gonads indicates a spawning season from March to September. Food is exclusively planktonic and the intake is greatest during the spawning months. In the autumn, spent fish build up a fat reserve to withstand the winter fast.

Went, A. E. J. (1945). 'Irish previously spawned salmon.' Sci. Proc. R. Dublin Soc. 24: 1–8.

Of 25,029 scales, one from each fish, 4·3 % were from previously spawned fish. Only twelve fish had spawned previously on two occasions and none had spawned three times. There is no evidence that very large salmon are 'returned kelts'; only two such fish over 35 lb. have been recorded in all the Irish fishery investigations.

Frost, W. E. (1945). 'The age and growth of eels (*Anguilla anguilla*) from the Windermere catchment area. Part 1.' J. Anim. Ecol. 14: 26–36.

Discusses the errors of interpreting age from otoliths and scales. Otoliths showing more than 7 or 8 years cannot be read with accuracy and scales from different parts of the eel may have different numbers of annual zones.

Frost, W. E. (1945). 'The age and growth of eels (*Anguilla anguilla*) from the Windermere catchment area. Part 2.' J. Anim. Ecol. 14: 106–24.

Age, determined by otoliths and/or scales, in relation to length and to weight is presented graphically and in tables for yellow (immature) and for silver (mature) eels. A small minority of female eels become silver when older and larger than the others. The mean time spent in fresh water by female silver eels is 12·27 years (from 9 to 19), their mean length is 60·8 cm. (from 47 to 95) and mean weight 410 g. (from 210 to 2040). Male silver eels comprise only a small proportion, are smaller (39·9 cm. mean length and 112 g. mean weight), and spend an average of 9 years in fresh water. The commonest length for females at migration is 54–60 cm., and it is suggested that length, not age, controls migration. The length-weight relationship does not follow the cube law, and is different in yellow and silver eels; it shows no definite trend with age. Growth is less rapid than in continental waters, due probably to environmental factors among which overstocking due to larger numbers of elvers entering British waters is suggested as a possibility.

Freeman, J. A. (1945). 'Studies in the distribution of insects by aerial currents. The insect population of the air from ground level to 300 feet.' J. Anim. Ecol. 14: 128–54.

The population of insects sampled at heights of 10 ft., 177 ft. and 277 ft. along a north-south front of 4400 ft. by nets flown from masts of a beam wireless station in level agricultural land in Lincolnshire was mainly small weak-flying insects of high buoyancy drifted involuntarily by the wind. Diptera were most numerous near the ground, Hemiptera above 100 ft., while Aphididae was the most numerous family at all heights. The species may be classified as 'aerial' and 'terrestrial'. Local vegetation determined the general character of the aerial fauna, which changed significantly from month to month, the greatest numbers occurring in May, June and September. Maximum numbers of most groups occurred at relative humidities below 59 %, wind of 12 m.p.h. or less, and temperatures above 64° F., the last factor exercising most control. In high winds collections were relatively small, and insects tend to seek shelter. The importance of moderate winds and wind drift, rather than storms, in dispersal is emphasized. Ground quarantines have been useless in preventing the spread of insects so easily drifted by wind.

Walsh, G. B. (1945). 'Reappearances of the wall butterfly, *Pararge megaera* L. (Lep., Satyridae) in northern England.' Ent. Mon. Mag. 81: 236.

This species is becoming common again in the north of England after an interval of very many years.

Stroyan, H. L. G. (1945). 'The decline of *Limenitis camilla* in a Surrey wood.' Entomologist, 78: 103.

In 1935 the total population of white admiral butterflies in a 100-acre wood was estimated (? how) as not more than 50–100 specimens. Two ab. *seminigrina* were seen in that year. The population declined rapidly after 1935, till by 1939 the species was nearly extinct in the locality. 'This seems to bear out the theory that increase in variation foretells the imminent decay of a population.'

Stokes, H. G. (1945). '*Limenitis camilla* L. and *Vanessa cardui* L. (Lep.) in Wiltshire.' Ent. Mon. Mag. 81: 236.

The white admiral butterfly observed in a small wood of conifers where it had not previously been found. This species has been extending its range.

Talbot, G. (1945). '*Nymphalis polychloros* in Surrey.' Entomologist, 78: 125.

The large tortoiseshell butterfly was not uncommon in the Wormley district of Surrey up to about 1920, but gradually disappeared. A specimen is reported from Hambledon on 5 July 1945.

Adams, C. V. (1945). 'Scarcity of *Nymphalis io* at Pendeen (West Cornwall) (Lep. Rhopalocera).' Proc. R. Ent. Soc. Lond. A, 20: 101–4.

Observations, together with results of liberating and recovering marked specimens, on the peacock butterfly.

Ford, H. D. (1944). '*Leucophasia sinapis* (the wood white) as a Cumberland species.' Rep. Lanc. Chesh. Ent. Soc. 64–7: 37.

This butterfly appears to have been taken occasionally as far north as the Carlisle district of Cumberland, but the records of its capture are scarce and old. The most recent record appears to be about 1900 in the Orton district, some five or six miles west of Carlisle.

De Worms, C. G. M. (1945). 'Melanic forms of *Xanthorhoë fluctuata*.' Entomologist, 78: 189.

Records of a dark common carpet moth at Horsell and Wimbledon. Asks if this form is spreading in the south.

Whelan, C. B. (1945). 'Irish distribution of *Biston betularia* L. ab. *doubledayaria* Mill.' Entomologist, 78: 174.

There are now four records of this dark variety of the peppered moth from Ireland. It originated in the north of England and is now widespread in Britain.

Gunn, D. L. & Knight, R. H. (1945). 'The biology and behaviour of *Ptinus tectus* Boie. (Coleoptera, Ptinidae), a pest of stored products. VI. Culture conditions.' J. Exp. Biol. 21: 132–43.

Details of how to breed uniform animals. Groups of larvae take longer to reach the adult stage and are then of smaller weight than animals brought up singly.

Richards, O. W. (1944). 'The two strains of the rice weevil, *Calandra oryzae* (L.) (Coleopt., Curculionidae).' Trans. R. Ent. Soc. Lond. 94: 187–200.

There are two strains of *Calandra oryzae* which differ principally in size (weight). Genetic factors affect weight considerably more than does the type of grain used. The two strains only cross with great difficulty and the hybrids appear to produce no visible offspring. The strains are nevertheless not regarded as species since there is no non-overlapping morphological difference or combination of differences between them. The strains differ in all the physiological characters which have been investigated, viz. length of life-cycle at 25° C., rate of sexual maturation, oviposition rate, resistance to starvation and ejection of frass by larva.

Birch, L. C. (1945). 'The biotic potential of the small strain of *Calandra oryzae* and *Rhizopertha dominica*.' J. Anim. Ecol. 14: 125–7.

The biotic potential, $E \times S/2D$, where $E =$ potential number of eggs laid, $S =$ percentage survival, and $D =$ days taken to develop from egg to adult, was calculated for the various temperatures and moisture contents in wheat at which the two species can multiply. The maximum number for each was 650. Curves of isopleths show that *R. dominica* multiplies more rapidly at higher temperatures and lower moisture content than *Calandra oryzae*.

Cockbill, G. F., Henderson, V. E., Ross, D. M. & Stapley, J. H. (1945). 'Wireworm populations in relation to crop production. I. A large-scale flotation method for extracting wireworms from soil samples and results from a survey of 600 fields.' Ann. Appl. Biol. 32: 148–63.

Size and composition of wireworm populations in grass and arable fields. Limitations of the hand-sorting method are pointed out.

Miles, H. W. & Miles, M. (1945). 'Changes in wireworm populations associated with cropping.' Ann. Appl. Biol. 32: 235–6.

The rate of decline of populations associated with a root crop is not greater than that associated with a cereal crop. There is a slow increase during the early years of populations in adjoining ley plots.

Arthur, D. R. (1945). 'On the ecology of the wireworm *Dolopius marginatus* L. (Col., Elateridae) in the South Wales Province.' Ent. Mon. Mag. 81: 205–12.

Only one species of wireworm has been found infesting the soils of South Wales. Its distribution in this region is markedly discontinuous and shows correlation with factors inherent in or influenced by the surface geology. Where the latter results in good natural drainage and light or light-medium loams the wireworm has been recovered. No consistent correlations have been found between other soil characters, i.e. pH, available phosphates, potash or vegetational cover.

Association of Applied Biologists (1945). 'Symposium on the carrot fly.' Ann. Appl. Biol. 32: 262–76.

Includes 'The biology and control of the carrot fly' [*Psila roseae*] by **F. R. Petherbridge, D. W. Wright** and **D. G. Ashby;** and 'The carrot fly in the Midlands' by **A. Roebuck.**

Milne, A. (1946). 'The ecology of the sheep tick, *Ixodes ricinus* L. Distribution of the tick on hill pasture.' Parasitology, 37: 75–81.

The nymphal population density in sheep lairs is significantly lower than, and that of sheep tracks similar to, that of the general pasture. If the vegetation layer becomes thinner, as is usual with increased altitude, nymphal density decreases. Ticks are not evenly distributed over apparently uniform areas of vegetation.

Jones, F. G. W. (1945). 'Soil populations of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping.' Ann. Appl. Biol. 32: 351–80.

Sampling technique and results of sampling 24 fields from 1937–42.

Barnes, H. F. & Weil, J. W. (1945). 'Slugs in gardens: their numbers, activities and distribution. Part 2.' J. Anim. Ecol. 14: 71–105.

Slugs in gardens feed on a large variety of substances of plant and animal origin, but only very little consists of plant material useful to man, except where there is only one crop, e.g. potato patches. Some species mate in the open, others require cover. Slugs show regular changes in weight throughout the year, and are heaviest soon

after the appearance of the greatest numbers and at the mating peak. The slug faunas of adjacent gardens often show extreme differences which are not related to soil reaction, organic carbon content or mechanical analysis, but may be influenced by topography and age of the gardens. There is evidence that each species has its own curve of nightly activity. Activity continues to near the freezing-point, is limited by lack of surface moisture, and reduced by heavy rain and strong wind. Optimum conditions are: a warm still night with plenty of surface moisture. Three coloured plates illustrate eight species, which include most of those of economic importance in England. This paper deals mainly with *Arion ater, A. circumscriptus, A. hortensis, A. subfuscus, Milax gracilis, M. sowerbyi* and *Agriolimax reticulatus*.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Barnes, J. A. G. (1945). 'The status of the lesser black-backed gull in north-west England and North Wales.' Brit. Birds, 38: 342–6.

Some evidence is given suggesting that *Larus fuscus* is resuming the habit of wintering in these areas, which it apparently gave up about the beginning of the century.

Williamson, K. (1945). 'Late blackcaps in the Faeroe Islands.' Northw. Nat. 20: 66–7.

Sylvia atricapilla recorded in Britain in the winter are evidently birds from north-western Europe whose migration has stopped short, not summer visitors that have not emigrated at the usual time. Migration as late as September and early October is common in this species, but in certain years it may take place almost a month later.

Clementson, G. (1945). 'Golden orioles near Peel.' Peregrine, 1 (3): 26–7.

Two *Oriolus oriolus* seen in the Isle of Man on 3 July 1944. There are only two previous records for the Island.

Calderwood, W. L. (1945). 'Passage of smolts through turbines: effect of high pressures.' Salm. Trout Mag. (Lond.) No. 115: 214–21.

Development of hydro-electric schemes in Scotland has raised the question whether migrating smolts of salmon and sea trout are affected by the changes in pressure involved in passage through turbines. Experiments showed that brown trout (*Salmo trutta*) $4\frac{1}{2}$ in. long were unaffected by rapid changes of pressure up to 72 lb. and sudden release to $7\frac{1}{2}$ lb. They were temporarily affected at 150 lb. but recovered when the pressure was lowered.

Collenette, C. L. (1945). 'Pieridae and sundews.' Entomologist, 78: 129–30.

In 1944 (Proc. R. Ent. Soc. Lond. A, 19:5) F. W. Oliver recorded about 6 million small white butterflies (*Pieris rapae*) caught by the long-leaved sundew (*Drosera anglica*). Experiments now described show that Pierids in flight are strongly attracted to others on the ground, irrespective of any other inducement. Although the proportion which actually settled was small, it might well be much larger if the insects were tired after a long flight.

Riley, N. D. (1945). '*Papilio machaon* in southern counties.' Entomologist, 78: 142.

Reports suggest that the swallow-tail butterfly may have accompanied the migrant wave of other species.

Kettlewell, H. B. D. (1945). '*Pontia daplidice, Everes argiades* and *Colias hyale* in South Cornwall.' Entomologist, 78: 123–4.

1945 was an astonishing year for immigrant butterflies: the Bath white oviposited freely in nature on the hedge-mustard *Sisymbrium officinale*. See also many other papers in 1945, Entomologist, 78, and Ent. Rec. 57, on this and other migrant Lepidoptera.

Fraser, F. C. (1945). 'British born and bred *Pontia daplidice* L. (Lep., Pieridae).' Ent. Mon. Mag. 81: 237.

An unprecedented immigration of the Bath white butterfly took place in 1945. 22 specimens were taken at Bournemouth from which a second generation was reared. See also **Perkins, R. C. L.** (1945), Ent. Mon. Mag. 81:216.

Ellison, N. F. (1945). 'Striped hawk moth in Wirral, Cheshire.' Northw. Nat. 20: 70–1.

Specimen of *Celerio livornica* taken near Birkenhead on 19 April 1945.

Nowers, J. E. (1945). '*Celerio livornica* Esp. in Darlington.' Northw. Nat. 20: 71.

Record of migrant striped hawk moth.

Chapman, F. W. (1945). 'Moths attracted by searchlights.' Entomologist, 78: 176.

On one night in August about 5000 *Plusia gamma* were encountered in and around a searchlight at Hastings. Observation with binoculars showed many Sphingidae at 50–100 ft. Only a few of these were taken at ground level, these being *Smerinthus populi* and *Mimas tiliae*.

Wilson, G. F. (1945). 'The leopard moth.' J. R. Hort. Soc. 70: 148–50.

Zeuzera pyrina is increasing in importance as a minor orchard pest, particularly on apple. Damage to 24 trees and shrubs, mostly fruit and ornamentals, has been reported from 20 English counties, notably Hampshire, London, Middlesex, Surrey and Sussex, during the past 12 years, and 12 other trees are known to be attacked. Feeding on horse-chestnut (*Aesculus hippocastanum*), which was thought to be a preferred food-plant, was less common than on fruit trees. Young trees, those with little sap and forest trees on poor soil are preferred. Green woodpeckers (*Picus viridis*) were the only natural enemies observed.

Anon. (1945). 'Colorado beetle in England during the war.' J. Minist. Agric. 52: 210–15.

Account of the 'invasions' of *Leptinotarsa decemlineata* at Whitstable in 1940, in the West Country coastal and inland areas in 1941, in Devon, Dorset and Wiltshire in 1942 and in Wiltshire in 1943.

Common, A. F. (1945). '*Coccinella septem-punctata* in Essex.' Entomologist, 78: 136.

Invasion along the sea front in July 1945, of this ladybird, similar to that noted in 1944. On the same day the large white butterfly (*Pieris brassicae*) and the hover fly *Syrphus balteatus* were also observed in large numbers.

Marshall, J. F. (1945). 'Records of *Culex* (*Barraudius*) *modestus* Ficalbi (Diptera, Culicidae) obtained in the south of England.' Nature, Lond. 156: 172–3.

Two females of this mosquito, collected on the Hampshire coast in July 1944, failed to survive in the laboratory. In August 1944 six larvae were found in a static water tank in Portsmouth. In May 1945 another female was found on the coast and, in June, four larvae in a pool of brackish water in Gosport. On incubation the larvae gave three males and a female, and the latter laid an egg raft. It is suggested that this immigrant, hitherto unrecorded north of Paris, arrived by aeroplane.

Wilson, G. Fox (1944). 'The yew scale.' J. R. Hort. Soc. 69: 244–8.

Lecanium crudum-corni was observed on conifers, probably for the first time, in Sussex in 1928 and was probably introduced from Western Europe. Its present known distribution on *Taxus baccata* in 14 counties of southern and eastern England is shown on a map; it is most widespread in Surrey and Sussex. Infested nursery stock, birds and wasps and bluebottle flies, which are attracted to the honeydew excreted by it, are considered to be the agents of dispersal. Winged males are freely produced from mid-May, but reproduction appears to be chiefly parthenogenetic.

7. REPORTS OF ORGANIZATIONS

Freshwater Biological Association of the British Empire (1945). Thirteenth Annual Report for the year ending 31 March 1945. 42 pp. Price to non-members, 1s. 6d.

Gives non-technical accounts of work in progress at Wray Castle on the ecology of char (*Salvelinus alpinus*), pike (*Esox lucius*), perch (*Perca fluviatilis*) and eels (*Anguilla anguilla*); on phytoplankton; and on lake deposits.

Éire, Department of Agriculture, Fisheries Branch, (1945). Report on the sea and inland fisheries for the year 1944. Dublin, 27 pp. Price 9d.

Abnormal floods and extreme cold resulted in a diminution of the output of both salmon and brown trout ova and delay in their development. 38 'hatching out' stations were operated. Generally, among both salmon and trout, there was no appearance of disease. The distribution of the char (*Salvelinus alpinus*), a comparatively rare fish, has been investigated. There are 16 appendices.

Wye Board of Conservators (1945). Annual Report, Season 1944. 11 pp.

A general account of the fisheries of the Wye giving statistics and notes on various factors. The salmon catch was low and the fish of low average weight. The prolonged drought affected fishing and there was a marked deficiency in 5-year-old fish, which influenced the catch and the average weight. Eel production, owing to drought followed by severe floods, was only about one-third of the previous year.

Salmon parr were observed migrating upstream in the autumn. Those caught for examination proved to be ripe males.

Ogg, W. G. (1946). 'Some aspects of the work at Rothamsted.' S. East. Nat. 50: 1–14.

A useful survey of the scope of this agricultural research institute.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1945

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance:		
Members taking *Journal of Ecology* only ...	278 12 6	
Members taking *Journal of Animal Ecology* only ...	161 6 2	
Members taking both Journals ...	153 15 0	
Associates ...	593 13 8	
Less Reserve allocated to second part of each Journal, not yet published ...	230 0 0	363 13 5
Interest on Investments ...	64 13 0	
Interest on Deposit Account ...	2 16 7	67 9 7
Journal of Ecology. Sales *less* Cost ...		18 15 10
Journal of Animal Ecology. Sales *less* Cost ...		2 1 6
Index to *Journal of Ecology*, vols. 1–20:		
Sales ...	4 12 0	
Less Expenses ...	19 2	3 12 10
		£455 13 5
Journal of Ecology, 1945, Part 1:		
Sales: 50% Current vol. 33, part 1 ...	234 1 3	
Back volumes and parts ...	109 17 0	
Reprints of papers... ...	7 7 2	
		£351 5 5
Journal of Animal Ecology, 1945:		
Sales: 50% Current vol. 14, part 1 ...	95 11 0	
Back volumes and parts ...	148 8 0	
Reprints of papers ...	15 15 0	
		£259 14 0

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing and Stationery ...	15 18 3	
Postages ...	8 2 7	
Travelling ...	8 7 0	
Wild Life Conservation Memorandum ...	14 15 0	
Meeting Expenses ...	6 12 6	
Audit Fee ...	6 6 0	
Bank Charges and Typing ...	18 0	
Clerical assistance ...	13 0 0	73 19 6
Grant: to Freshwater Biological Association ...		10 0 0
Subscription: to Parliamentary and Scientific C'tee ...		10 10 0
Biological Flora of the British Isles:		
Costs of Printing, Commission, &c. ...	62 13 8	
Less Sales of Reprints ...	18 1 5	44 12 3
Balance—Surplus for the Year (To Balance Sheet) ...		139 1 9
		316 11 8
		£455 13 5
Journal of Ecology, 1945, Part 1:		
Costs: Vol. 33, part 1		
Paper, Blocks, Printing and Binding ...		267 0 0
Publishers' Commission ...		49 4 6
Carriage, etc. ...		8 5 1
Insurance of Stock ...		8 0 0
		332 9 7
Balance (see above, under Income) ...		18 15 10
		£351 5 5
Journal of Animal Ecology, 1945:		
Costs: Vol. 14, Part 1		
Paper, Blocks, Printing and Binding ...		199 9 2
Publishers' Commission ...		34 16 5
Carriage, etc. ...		5 6 11
Insurance of Stock ...		8 0 0
Fee for checking references ...		10 0 0
		257 12 6
Balance (see above, under Income) ...		2 1 6
		£259 14 0

BALANCE SHEET AT 31 DECEMBER 1945

Assets

	£ s. d.	£ s. d.
Cash at Bank: Current Account	606 18 1	
Deposit Account	100 0 0	706 18 1
Publishing Accounts—Amounts due from Cambridge University Press:		
Journal of Ecology. Balance of Account	276 19 2	
Journal of Animal Ecology. Balance of Account...	105 15 8	
Journal of Ecology. Index Volume ...	3 12 10	
Biological Flora of the British Isles	15 5 3	401 12 11
Investments at Cost:		
Held 31 December 1944—		
£1,200 of 3½ % War Loan	1,230 4 1	
£700 of 3 % Savings Bonds, 1960/70	700 0 0	
Purchased 9 June 1945—		
£300 of 3 % Savings Bonds, 1965/75 ...	300 0 0	2,230 4 1
		£3,338 15 1

A further Asset, not valued, is the Unsold Stock of Journals, Index Volume and Biological Flora Reprints held by the Publishers for the Society.

VICTOR S. SUMMERHAYES
ALEX. S. WATT
Hon. Treasurers.

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1946/7... ...		17 1 9
Library Fund		1 5 0
Printing Accounts due to the Cambridge University Press:		
Journal of Ecology, Balance of Account	33 19 9	
Sundry Printing and Stationery	36 4 0	70 3 9
Subscription due to Parliamentary and Scientific Committee		10 10 0
Grant towards paper in Journal of Animal Ecology ...		100 0 0
Reserve of Subscriptions for 1945 allocated to second part of each Journal...		230 0 0
General Revenue Account—Surplus in Hand:		
Balance at 31 December 1944	2,593 2 11	
Surplus for year 1945	316 11 8	2,909 14 7
		£3,338 15 1

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants.

120 BISHOPSGATE, E.C. 2
and
231a HIGH ROAD, LOUGHTON, ESSEX.
6 March 1946.